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Germination, survival, and early growth of three invasive plants in response to five forest management regimes common to US northeastern deciduous forests

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ABSTRACT

The association between invasive plants and disturbance is well-documented. Most forest management regimes include disturbance (i.e., harvesting and fire) to improve regeneration of native plants, such as oaks. There is a need for land managers of northeastern forests to foster regeneration of native species without promoting invasive species establishment. We evaluated the germination, first-year survival, and growth of three exotic plants (*Ailanthus altissima*, *Alliaria petiolata*, and *Microstegium vimineum*) in 56 uninvaded forest stands located in five management regimes (control, single burn, repeat burn, diameter limit cut, and shelterwood) across two provinces (Appalachian Plateau, AP, and Ridge and Valley, RV) and two slope aspects (north-to-east facing, NE, and south-to-west facing, SW). These results were compared with the native *Quercus rubra* survival and growth under the same conditions. Two-hundred-fifty seeds and 30 transplants for each species were planted at each site. Germination, survival, and growth were measured three times over one growing season and analyzed using generalized linear mixed models.

RV sites had more open canopies, lower soil fertility, and lower plant species richness than AP sites; NE aspects had higher soil fertility and plant species richness than SW aspects. The shelterwood sites had the most open canopies. Germination rates were below 25%, but lowest in the control sites and higher in the RV and on NE aspects for all three species. Survival was above 70% for *A. altissima*, *M. vimineum*, and *Q. rubra* but below 20% for *A. petiolata*, with little difference among province, aspect, or management regime for all three species. Survival decreased significantly between measurements. *Microstegium vimineum* grew the most of the three species. *Microstegium vimineum* and *A. petiolata* grew best in shelterwoods and better in the RV and on NE aspects. *Ailanthus altissima* had more root growth in the RV than the AP and the least root growth in the control sites. *Quercus rubra* survived better in the RV and best in the harvested sites, though growth did not differ among the management regimes. These invasive species are similar to many native species during the early stages of colonization; their germination, survival and growth are initially precarious and dependent on adequate resources (NE aspects) with minimal competition (RV province). Our results suggest that the likelihood of colonization by invasive plants could be reduced by keeping canopy openings below 15% and encouraging native understory competition with deer exclusion and artificial regeneration where native seed sources are depleted.

1. Introduction

The opening of a forest canopy after a disturbance, such as a harvest or fire, may result in invasion by exotic plant species, given a seed source (Hobbs, 1991; Hobbs and Huenneke, 1992; Eschtruth and Battles, 2009; Driscoll et al., 2016). Successful invasion of nonnative invasive plants in disturbed areas is further dependent, in part, on available resources, with mesic and nutrient-rich sites invaded more frequently than xeric sites (Davis et al., 2000; Huebner and Tobin, 2006). When making predictions about invasion by nonnative plants into forests, it is important to distinguish between invasion at the early colonization stage and invasion as measured in terms of the probability

Abbreviations: *AiAl*, *Ailanthus altissima*; *AlPe,*, *Alliaria petiolata*; AP,, Appalachian plateau; C, control; dbh, diameter at breast height; DLC, diameter limit cut; *MiVi*, *microstegium vimineum*; *QuRu*, *quercus rubra*; RB, repeat burn; RV, Ridge and Valley; SB, single burn; SHW, shelterwood

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of dominance and spread. For instance, Huston (2004) concluded that the probability of dominance is highest under productive conditions, whereas early establishment is more likely under unproductive, undisturbed site conditions or disturbed, productive site conditions. Theoretically, one could reduce invasion likelihood by manipulating the degree of disturbance or site productivity (Huston, 2004).

Successful oak regeneration in northeastern US forests is associated with forest management defined by disturbances that increase the amount of light reaching the forest floor and decrease competition with other plants. Historically, fire sustained some oak forests (Abrams, 1992) and current National Forest Plans in the Eastern US propose increasing the use of fire and/or shelterwood harvest treatments to sustain or restore oak ecosystems (Wayne National Forest Management Plan, 2006; Monongahela National Forest Management Plan, 2011). Shelterwoods are usually conducted with a first-removal harvest to open the canopy enough (anywhere between 30 and 70% residual basal area) to stimulate regeneration, followed by a second harvest that removes the remaining canopy trees (Loftis, 1990). Diameter limit cut (DLC) harvests are commonly carried out on private nonindustrial lands in the eastern US, which includes 75.5% of northeastern forests (Oswalt et al., 2014). Although DLC harvests usually result in a profit for both buyer and seller with harvests every 15–20 years, they may lead to a loss of valuable species and diminishing economic return on harvests over time (Nyland, 1992; Nyland, 2005; Kenefic et al., 2005). Regeneration prescriptions involving shelterwood harvests have been used by the US Forest Service, some state forests, and some large industrial forestry companies, but are less common on private lands because it usually takes 5–10 years before adequate regeneration is achieved and a more complete overstory harvest can be conducted to yield additional revenue (Brose et al., 1999a; 1999b). If a stand is not dominated by trees with diameters meeting the diameter limit or larger, DLC harvests may have lower or similar light levels reaching the understory than would be found in a first-removal shelterwood.

Fires used for oak regeneration in northeastern forests are generally low-intensity burns that open the subcanopy, reducing competition from shade-tolerant species (Lorimer et al., 1994; Miller et al., 2004; Hutchinson et al., 2005b). Fire behavior and, thus, plant species' response to fire can vary substantially across microclimatic gradients (Iverson et al., 2004; Iverson et al., 2008). Fire effects on herbaceous species composition of northeastern forests are significant, but show minimal post-burn increases in nonnative invasive plants (Hutchinson et al., 2005a) mainly in unproductive areas with invasive plant seed sources (Marsh et al., 2005). Unlike fire, increased nutrient availability after harvesting will be due to reduced nutrient uptake (Boerner and Sutherland, 1997) and slash decomposition, but not as much as would be found in ash after a fire (Belleau et al., 2006). Light levels are also likely to be higher after a harvest than a fire (Miller et al., 2004). Nonetheless, both fire and harvesting treatments result in a mosaic of microclimates in the understory. In areas prone to acid deposition, fire, unlike harvesting, may have a positive effect on general plant growth by increasing soil Ca/Al ratios (Boerner et al., 2004).

The positive correlation between disturbance and invasion by nonnative plants suggests that managing for oak regeneration with disturbance may elevate the risk of invasion. Our research addresses this oak regeneration and invasive plant establishment dilemma by focusing on responses of three common nonnative invasive plants of northeastern forests to disturbance-induced changes in available resources (e.g., light, water, nutrients) over a gradient of existing environmental conditions (physiography and vegetation composition). These environmental conditions influence nonnative invasive plants' ability to become established. Relating invasive plant response to both existing physiographic characteristics and changes in resource availability caused by fire or harvesting will help managers prioritize sites for both oak and invasive plant management. Because the effects of disturbance tend to be site specific and potentially less important than site abiotic and biotic conditions (Moles et al., 2012), this project encompasses both landscape and microclimatic scales in order to make our results relevant to more land managers of northeastern forests. Our research links resource changes caused by common forest management regimes to nonnative invasive plant early establishment and productivity along both small-scale topographic and large-scale physiographic gradients. All in all, we address the possibility of manipulating disturbance severity or existing environmental conditions (perhaps by selecting certain site types over others) in such a way to reduce the risk of invasion in response to forest management regimes used to regenerate native species.

Microstegium vimineum (Japanese stiltgrass), hereafter referred to as *MiVi*, *Alliaria petiolata* (garlic mustard), hereafter referred to as *AlPe*, and *Ailanthus altissima* (tree of heaven), hereafter referred to as *AiAl*, are among the more aggressive nonnative plant invaders of northeastern forests of the US, but are also of international significance as invaders. *MiVi*, native to Asia, is also found as a nonnative species in Central America and the Caribbean (EPPO, 2015). *AlPe*, native to Europe, is also found as a nonnative plant in Canada and Australia (CABI, 2017). *AiAl,* native to north and central China, Taiwan, and North Korea, is considered a problematic exotic nationwide in the US and is now also present as a nonnative species in Canada, Europe, eastern Asia, Africa, Central America, South America and both Australia and New Zealand. (Q-Bank, 2017).

Both *MiVi*, an annual late-season grass, and *AlPe*, a biennial herb, are shade-tolerant species often found in closed-canopy conditions, making them a threat in highly disturbed and less disturbed forests. Though shade-tolerant, *MiVi* produces significantly less seed in shaded environments, primarily due to a smaller plant size (Huebner, 2011; Cheplick and Fox, 2011) and lower abundance (Beasley and McCarthy, 2011). *MiVi,* which uses C_4 photosynthesis, can rapidly grow and produce more seed in response to small increases in light, such as sunflecks or canopy gaps, but it can only use 25% of full sunlight (Winter et al., 1982; Horton and Neufeld, 1998). Glasgow and Matlack (2007) showed that *MiVi* abundance was significantly greater after a high-intensity burn than low-intensity burn or no-burn in mesic valleys but only under canopy gaps, suggesting that this species' local abundance is most dependent on light availability. *AlPe* flowers once in early spring of its second year, taking advantage of the relatively open forest canopy. Similar to *MiVi*, *AlPe* may be found in high-light and shaded areas. *AlPe* can be found at higher densities in closed canopy conditions, but its second year of growth and reproduction appears to be most stimulated by intermediate light levels (Byers and Quinn, 1998; Phillips-Mao et al., 2014). *AiAl* growth rates are significantly higher in high-light environments than in low light, though small seedlings and saplings will survive under a closed canopy and low-light conditions (Kota et al., 2007). Similar to *MiVi*, *AiAl* responds positively to an increase in light, and its response will be most evident in high-light conditions. Of the three species, both *MiVi* and *AlPe* appear to be relatively dependent on mesic conditions. *AiAl*, a dioecious tree, is relatively drought tolerant and may invade more xeric sites (Trifilo et al., 2004). Though most females of *AiAl* usually do not produce seed until they are small trees (Wickert et al., 2017), both sexes will spread prolifically via root sprouts. Vegetative growth of this species increases in response to stem and root damage (Kowarik and Säumel, 2007).

Both *AlPe* and *MiVi* have been documented to form seed banks (Gibson et al., 2002; Byers and Quinn, 1998), which are likely to respond positively to any increase in light and nutrients resulting from a fire or harvesting. *AiAl's* high germination rates may explain a lack of a seed bank, but a seed bank has been found in several sites (Kostel-Hughes et al., 1998; Redwood et al. and Rebbeck unpublished data) where site conditions (lower temperatures) may affect germination as well as seed decomposition rates. Even without a long-lived seed bank, *AiAl*'s wind-dispersed seed may access new disturbed areas from as far away as 100 m (Landenberger et al., 2007), and once at these sites, may take advantage of the higher light and nutrient levels.

We asked the following question: How do *MiVi*, *AlPe*, and *AiAl*

respond to shelterwood versus diameter limit cut harvests versus fires of different frequencies in terms of their ability to germinate, survive, and grow in the early stages of establishment relative to the native *Quercus rubra* (northern red oak), hereafter referred to as *QuRu*, and does their response differ across ecoregions (provinces) or local topographies? Because all three nonnative species are potential regional, national, and global invaders and all three are known to invade forested areas, understanding their likely response to different forest management regimes will be of national and global interest and will improve our ability to predict invasive plant establishment and the likelihood of spread. Likewise, determination of the relative response of these nonnative species compared with the response of the native species for which these management regimes were designed will enable forest managers to predict the likelihood of success of oak regeneration compared to that of invasion by nonnative plants.

2. Methods

2.1. Study area

Our study took place in the unglaciated Appalachian Plateau (AP) and Ridge and Valley (RV) physiographic provinces of the eastern US (Fig. 1). The AP province is characterized by high plains of shale, siltstone, sandstone, and limestone; the RV province is characterized by longitudinal ridges of sandstone and conglomerate sedimentary rock with continuous valleys of limestone and shale in between (Bryce et al., 1999). The AP province receives 1010 (eastern OH) -1270 (western WV) mm or more precipitation annually. Because of a rain shadow effect, the RV province receives 760–830 mm of precipitation (Abrams and McCay, 1996; Kozar and Mathes, 2001; Ohio Department of Natural Resources (ODNR), 2011). The average daily temperatures in July are 20.6° C and 21.4° C for the AP and RV, respectively (Clarkson, 1964; Pyle et al., 1982; Estepp, 1992; Abrams and McCay, 1996). The sites located in the drier and warmer climate of the RV are characterized by *Quercus* spp., *Carya* spp., and *Pinus* spp. with *Acer rubrum* increasing since the loss of *Castanea dentata* to chestnut blight. Sites in the more mesic AP province are associated with *Fagus grandifolia*, *Acer saccharum*, *Betula* spp. and *Tsuga canadensis* with increases in *Prunus serotina*, *Acer rubrum* and *Betula* spp. since the loss of *C. dentata* (Clarkson, 1964; Abrams and McCay, 1996). Sites were located on federal, state, and private land; those on private land were owned by industrial wood products companies as well as single families. Site GIS coordinates are provided in Huebner and McGill (2018).

2.2. Experimental design

We located sites in five existing forest management regimes that represent those common to both provinces. These management regimes included: (1) no management (control sites) of forests at least 70 years of age, (2) single prescribed burn of forests at least 70 years of age, with a single burn within five years of the beginning of this study, (3) repeat prescribed burns of forests at least 70 years of age, with at least two burns within the five years of the beginning of this study, (4) a 2–4 year-old diameter limit cut (DLC) harvest with 50–75% of the total basal area of merchantable trees ≥16–18 in. in diameter removed (i.e., removing the largest trees; largest remnants trees were at least 70 years of age), and (5) a 3–4 year-old first-removal shelterwood harvest with 50–75% of the overstory basal area from trees of mixed sized classes removed (largest residual trees were at least 70 years of age). Trees were aged from three cores taken from the largest trees at each site using WinDENDRO 2009a (Regent Instruments, www.regentinstrument.com; www.regent.qc.ca) and these values confirmed the site age estimates from the available site history. Prior to the current management, each site was likely harvested at least once as part of the

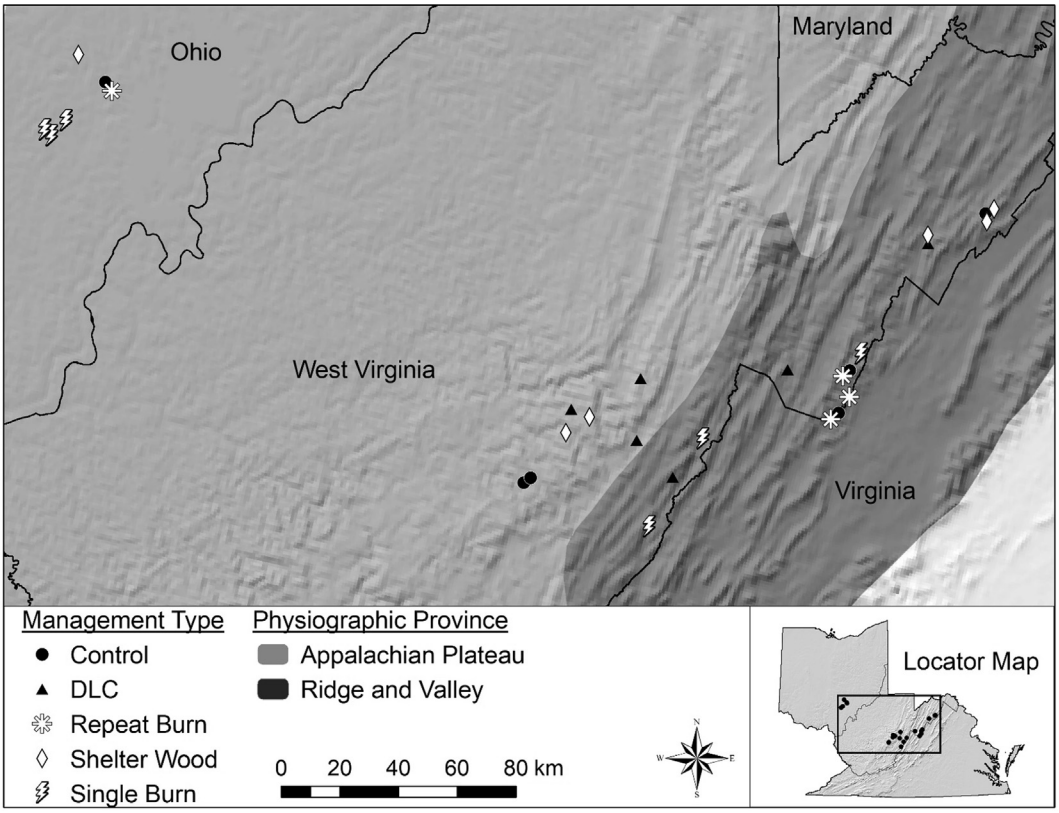

Fig. 1. Study area. Study area showing the 56 sites (some overlapping) across the two physiographic provinces. As part of the Appalachian Plateau, there are 14 sites in WV and 12 sites in OH; as part of the Ridge and Valley, there are 28 sites in WV and two sites just across the border in VA. DLC = diameter limit cut harvest. Each point represents the paired NE and SW slopes; hence only 28 points are showing. Stands do not overlap; any overlap visible on the map is due to scale.

extensive land clearings (clear cuts and fires) for railways that took place in the early 1900s in this region, with most fires being started by locomotives in WV (Brooks and White, 1910) and to supply the charcoal iron industry in OH (Stout 1933).

Our design was to locate three replicates of each management regime on paired northeast (NE)- and southwest (SW)-facing slopes in both the AP and RV provinces, resulting in 60 sites (3 replicates × 2 slope aspects × 2 provinces × 5 management regime = 60). However, two planned repeat burns (including the paired aspects or a total of four sites) in the AP province did not take place in time for our study, resulting in only one repeat burn (paired NE and SW aspects or two sites) for the AP province or a total of 56 sites. Replicate sites were randomly selected from available sites within each category that met all the criteria and were free of the three invasive plants species. Slope inclination averaged 34.9% for the AP and 37.7% for the RV. Elevations averaged 623 m (250 – 1200 m) for the AP and 805 m (585 – 1260 m) for the RV.

2.3. Vegetation data

At each site, a 100-m transect that ran along the elevational contour in the middle of the stand was set up with four circular 1-m^2 plots, nested within ten circular 10-m^2 plots located every 10 m along the transect (Fig. 2). Every other 10-m^2 plot was fenced using 2-m tall galvanized hexagonal metal poultry fencing; the plots were small enough to prevent deer from being able to jump into the fenced area. In each 1-m^2 plot, percent cover of all herbaceous species, vines, and shrubs was estimated to the nearest 0.5%, and both cover and density were measured for all the tree seedling species. Cover of herbs was only included if the herbs were rooted in the plot, but shrub and vine cover was included without the requirement of being rooted inside the plot. Tree seedlings were defined as any tree species less than 1-m tall; only seedlings that were rooted in the plot were included. Average cover per plot for each species of the herbs, vines, and shrubs was determined at each site. These were also totaled into a total herb, vine, and shrub cover and averaged per plot. Average cover and average density per plot were determined for each tree seedling species and averaged for each tree species. Average understory species richness and diversity (Shannon-Weiner index) per plot were calculated for each site. Leaf litter depth (to mineral soil or rock) was measured at the western edge of each 1-m^2 plot (an arbitrary location selected to prevent any bias). All tree saplings, defined as 1-m or taller and under 10-cm diameter at breast height (dbh), were counted in the ten 10-m^2 plots. Sapling counts were averaged per plot for each site. Tree dbh was measured for each tree 10 cm or greater dbh within two 1000-m^2 plots that dissected the transect (Fig. 2) and total tree basal area per site was calculated for

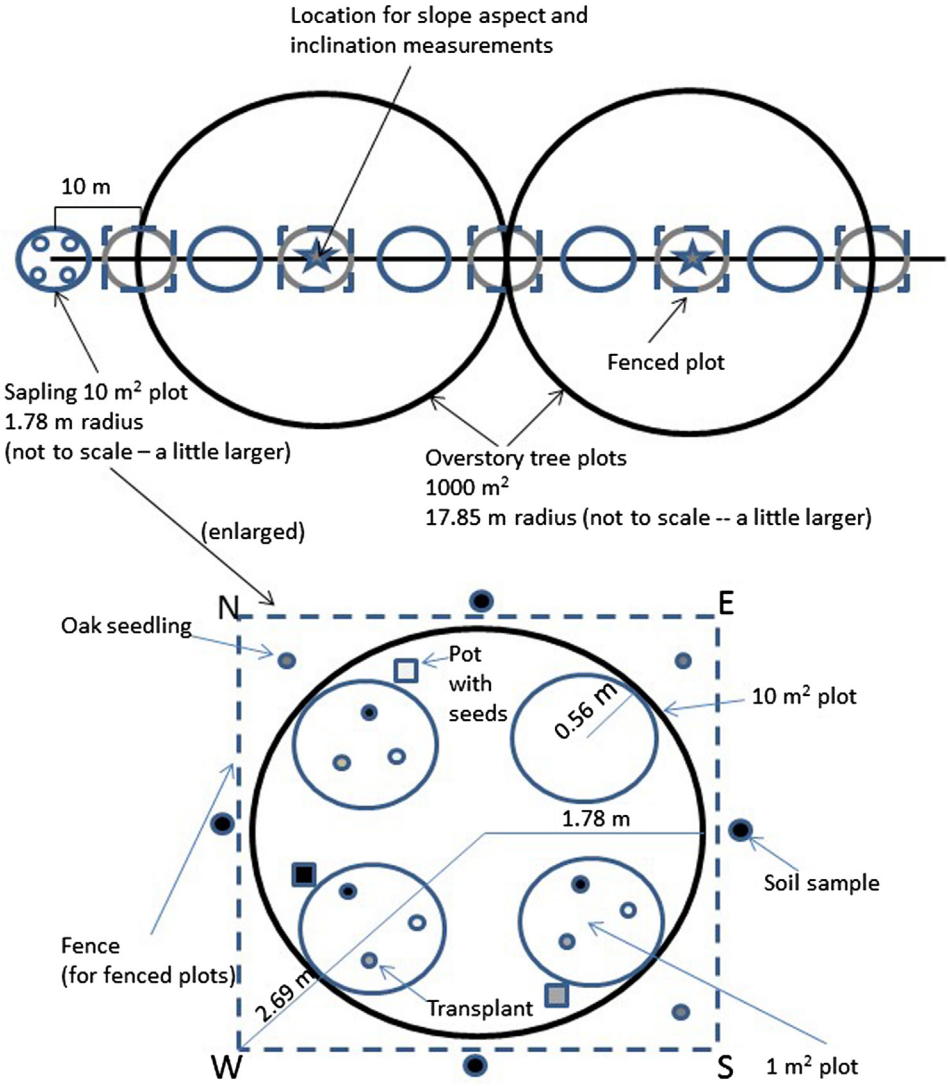

Fig. 2. Main transect and plots. The 100-m transect showing the locations of the herb/shrub/vine/tree seedling (1-m^2), sapling (10-m^2), tree (1000-m^2) plots, the locations of the germination pots (square), the three exotic plant and oak transplants, and the soil samples.

each species. All vegetation and litter data were collected between June and August 2010.

2.4. Soil and light data

A soil sample was taken at each cardinal direction outside each 10-m^2 plot and always outside each fence. Soil was collected June - August 2010 from the top 10 cm in the odd numbered plots and from the first 10 cm of the B-horizon (horizons above B were removed from the sample) in the even numbered plots using a 2-cm diameter soil auger. Because both the 10-cm depth and B-horizon samples produced similar results, we present only the 10-cm depth soil (soil volume of 31.4 cm^3) data, but results for the B-horizon samples can be found in Huebner and McGill (2018). Soil analyses included soil pH, percent soil organic material, percent total nitrogen and carbon, concentrations (mg/kg) of Ca, K, Mg, P, Al, Mn, Zn), and cation exchange capacity (CEC) measured in meq/100 g (Maine Analytical Laboratories, University of Maine, Orono, ME).

In the center of each 10-m^2 plot, percent canopy opening was determined using a fish-eyed lens hemispherical photograph June -July 2011. Photographs were analyzed for percent canopy opening using HemiView 2.1 (Delta-T Devices Ltd 1999, Cambridge, UK) and averaged for each site. Red:far-red using a LightScout red:far-red meter (Spectrum Technologies, Inc. Aurora, IL) was measured in the center of each 10-m^2 plot twice (June/early July and July/early August) at each site. Both gave similar results, but the second had fewer missing data due to rain days, so only the second measures are presented. We used the red:far-red measures for relative comparisons between the provinces, aspects, and among the five management types. Though the red-far measures may have differed each day, time or under different degrees of cloudiness, the same was true for each province, aspect, and management type. Photographs and red-far-red measurements were taken at a height of 1-m. At the center of each 1-m^2 plot, the soil temperature was measured using a Reotemp soil thermometer (°C) (Reotemp Instruments, San Diego, CA) in late June/July. The 40 temperature readings were averaged for each site.

2.5. Seed germination trials

In each 1-m^2 plot (Fig. 2) three 10 cm wide × 10 cm tall square pots were buried (one pot for each invasive plant species), keeping soil and litter intact and the top of the pot just visible above the ground. Twenty-five seeds of each species were placed under the litter layer in their respective pots for a total of 250 seeds per species per site (Fig. 2). Planted seeds had an equal chance of seed predation, but are not a preferred food by rodents (Ostfeld et al., 1997; Cassin and Kotanen, 2016). All seeds were collected the previous year (early August 2010 for *MiVi*, early October 2010 for *AiAl*, and late June 2010 for *AlPe*) from locations nearby our sites within their respective provinces (AP or RV). Only RV seeds were planted in RV sites and only AP seeds were planted in AP sites. Seeds were stored in a refrigerator at 4 °C until time of planting. This temperature provides a cold stratification for *MiVi* and *AiAl*; cold stratification is not required for either species but does tend to improve germination rates (Graves, 1990). *AlPe* requires a cold, moist stratification in organic medium for germination (Raghu and Post, 2008). Seeds for all three species were planted in late May and early June. Because of *AlPe*'s requirements of a moist-cold stratification for germination, germination tallies for this species could not begin until the following year, after they overwintered. Germination tallies were a count of the number of germinants out of the total planted in each pot. Germination of *MiVi* and *AiAl* were tallied in both June and July 2011. Germination tallies for *AlPe* were conducted in both June and July 2012. The two tallies enabled us to see if germinations occurred earlier, later, or over a longer period than a few weeks. Acorns were not planted to determine *QuRu* germination rates because it would be impossible to adequately control for acorn predation across these 56 sites.

2.6. Transplants

Cold stratified *MiVi* and *AiAl* seed collected from the same locations described under 'Seed germination trials' were germinated in plug (each plug 2 cm × 3 cm) trays filled with propagation mix soil (Fafard Superfine Germination Mix; SunGro Horticulture) in two Conviron walk-in growth chambers under 150 μmol m^{-2} s^{-1} PAR with a red/far red ratio of 0.64 (using Roscolux Cinegel blue light filter number 4260; Rosco industries), 65% (day) and 60% (night) humidity, and at temperatures of 25 °C/15 °C and 25 °C/25 °C, respectively, in mid-April. Germination generally took place about two weeks after planting the seed. Germinants were allowed to form the first set of leaves (two weeks after germination) before transplanting in early May. *MiVi* tends to have higher germination rates using colder night temperatures, whereas *AiAl* has higher germination rates with more uniform warm temperatures (Huebner, Pers. Obs.). The *AlPe* seed collected from the same locations above were planted in petri dishes filled with the same propagation soil and saturated with water. The petri dishes were then placed in covered trays for complete darkness, refrigerated at 4 °C, and kept moist for 120 days from mid-December 2010 until mid-April 2011, when the germinants with cotyledons were planted directly from the petri dishes. This mimicked germination conditions observed for these species in our study area, in which *AlPe* typically germinates in late April, whereas *MiVi* and *AiAl* germinate in early May. Three individuals of each species were planted within three of the four 1-m^2 plots (Fig. 2), totaling 30 individuals per species per site. The fourth 1 m^2 plot was left as a measure of impact of planting or treatment disturbance on the understory vegetation. Planting was done using a dibble and then spraying the transplanted seedling plug with water in order to remove any air pockets, generally saturating the soil around the transplant in about a 2-cm radius. This is the only time water was added to the transplanted seedlings.

Three 1 + 0 (1 year in a seedling bed and 0 years in a transplant bed) *QuRu* seedlings were planted at each N, E, and S corner (fence gates were generally located at the W corner). The *QuRu* seedlings were purchased from Clements State Tree Nursery in West Columbia, West Virginia in March 2011 and stored at 4° C until planting. These seedlings were of unimproved stock and grown from seed collected throughout WV and southern OH. As this is within the extent of the study area, uncertainty in precise provenance was deemed acceptable. Planting of the oaks took place in late April and, due to the labor and time required, was done for two of the three replicates of each management regime, province, and aspect combination for a total of 40 sites. Water was also added only one time immediately after the planting.

2.7. Growth measurements

MiVi tends to branch and the lower branches will root at the nodes forming tillers, giving the appearance of multiple stems. Height for *MiVi* was measured as the base to the apex of the last fully formed leaf of the tallest tiller. If this tiller was damaged, the next tallest tiller was measured. *AlPe*'s height was measured from the base of the rosette (ground level) to the tallest leaf base (point of attachment to the leaf petiole). Height for *AiAl* was measured from the base of the main stem to the terminal bud. If the main stem was damaged, the tallest lateral stem was used. The number of leaves on the tallest stem, the total number of leaves, and the number of leaves on the main stem were determined for *MiVi*, *AlPe*, and *AiAl*, respectively. Oak seedling height was measured to the terminal bud of the main stem. If the main stem was damaged, the tallest lateral stem or branch was used and measured to its terminal bud.

Measurements were taken every five weeks between May and August 2011 with a total of three measurements at each site, including

the first measures at the time of transplant. Growth was determined for two time periods by subtracting the first measure from the two subsequent measures. At the end of August, both the root and shoot tissue of each surviving individual of each of the three nonnative species was removed and shoot biomass determined. Because it was not possible to distinguish the roots of *MiVi* and *AlPe* with certainty from that of other species growing in the plots, we did not determine their root biomass. However, *AiAl* has very distinctive bright white, somewhat rubbery-textured roots that can be differentiated from other roots, which made it possible to determine its root biomass. All biomass samples were dried for two days at 65 °C. The nonnative plants were removed within one growing season to prevent spread.

All plots were revisited for three years after the removal in 2011 to check for escapes. Two escapes (one *MiVi* and one AiAl) were found and removed. Both were associated with the buried germination pots. Oak seedlings were not removed and were measured for another growing season for another part of this study not presented here. Herbivory, by invertebrates for the invasive species, and both invertebrates and deer for the oaks, was classified as either being present (value of 1) or not (value of 0) and averaged across each site for each species as an average proportion of plants of each species that experienced herbivory. Herbivory data were combined for both the fenced and unfenced plots to determine general estimates of invertebrate and deer herbivory. Deer herbivory on *QuRu* in the fenced vs. unfenced plots was evaluated separately.

2.8. Data analyses

Soil C:N and Ca:Al, and percent organic carbon along with concentrations of K, Mg, P, Mn, and Zn were used as indicators of soil fertility (Cronan and Grigal, 1995, Knops and Tilman, 2000). Herb, tree seedling, sapling, live and standing-dead tree species richness, total herb, shrub, and vine cover, sapling and live and standing-dead tree density, and live and standing-dead tree basal area were calculated for each site. Diversity values were also calculated using both the Shannon-Weiner and Simpson indices, but served only to support the richness data (Huebner and McGill, 2018) and, thus, are not presented here. Each soil variable, canopy opening, red:far-red, total herb, shrub, and vine cover, herb, tree seedling, sapling, live and standing-dead tree richness, live tree and standing-dead tree density and basal area, and herbivory variables were included as separate response variables in individual generalized linear mixed models with site as the random effect and province, aspect, management regime, and the interactions of province, aspect, and management regime as fixed effects (Proc GLIMMIX; SAS 9.4 2013, Cary, NC, USA). Canopy opening, Ca:Al, percent soil organic material, concentrations of soil Mg, Mn, Fe, litter depth, soil temperature, total herb, shrub, and vine cover, herb, tree seedling, sapling, live tree, and stand-dead tree richness, and live tree and standing-dead tree density were best fit using a lognormal distribution and identity link function. C:N, CEC, soil pH, soil P, K, and Zn concentrations, red:far-red, and herbivory were best fit with a normal distribution and identity link function. Interactions were evaluated using least-square means comparisons with a Tukey adjustment and pdiff statement. Distributions were confirmed using a univariate analysis for each response variable (Proc Univariate; SAS 9.4 2013, Cary, NC, USA).

Percent germination of each species did not meet the assumptions for normality before or after transformation. The nonparametric Wilcoxon scores and Kruskal-Wallis test using the DSCF (Dwass, Steel, Critchlow-Fligner) option in SAS 9.4 (2013, Cary, NC, USA) were used to test for differences between the provinces and aspects and to make multiple comparisons among the management regimes (Critchlow and Fligner 1991). Percent survival, shoot height (*AiAl*, *MiVi*, and *QuRu*), leaf number (*AiAl*, *MiVi*, and *AlPe*), stem diameter (*QuRu*), and shoot and root biomass (*AiAl* only) data all met the assumptions of normality and were analyzed using a generalized linear mixed model with site as the random effect and province, aspect, management regime, and their interaction as fixed effects. Models were run separately for each species with a normal distribution and identity link function as the best fit model. Distributions were confirmed using a univariate analysis for each response variable (Proc Univariate; SAS 9.4, 2013, Cary, NC, USA). The two measurements taken for all survival and growth differences from the initial measures of the transplants were further compared using a generalized linear mixed model (normal distribution with identity link function) with site as a random effect and province, aspect, management type, measurement time, and their interactions as fixed effects, using an autoregressive (AR(1)) covariance structure to account for the repeated measures. Lastly, we compared differences in shoot growth and stem diameter (as separate response variables) for *QuRu* between the fenced and unfenced plots using generalized linear mixed models with a normal distribution and identity link function separately for province, aspect, management regime, and interactions. All generalized linear mixed models were run using Proc GLIMMIX in SAS 9.4 (2013, Cary, NC, USA).

3. Results

3.1. Light, soil, and vegetation characteristics of province, aspect, and management regime

As expected, the shelterwood and DLC sites had significantly greater canopy opening ($F = 10.8$, $P < 0.0001$) than the control sites. The shelterwoods had the highest soil K concentrations of all the management regimes and was significantly higher than the DLC harvests ($F = 3.5$, $P = 0.03$), while the single-burn sites had significantly higher soil pH than the control sites ($F = 4.6$, $P = 0.01$). The shelterwood and DLC sites also had higher soil temperatures and the shelterwoods and repeat burns had the shallowest litter depths of the five management types, though neither soil temperature or litter depth differences were significant. Also as expected, the management regimes differed for live tree richness ($F = 4.9$, $P = 0.007$), density ($F = 10.4$, $P = 0.0002$), and basal area ($F = 21.60$, $P < 0.0001$) with shelterwoods having significantly less of each than the control, single and repeat burn sites. The shelterwood sites also had significantly lower live tree density than the DLC sites. The repeat burns had significantly less live tree basal area than the control and single burn sites but not the DLC and shelterwood sites. The management regimes also differed significantly in terms of herb, shrub and vine cover ($F = 2.8$, $P = 0.05$), with shelterwoods having higher cover values than the control sites (Appendix 1).

Canopy opening of sites in the RV province was significantly greater than that of the AP province ($F = 19.6$, $P = 0.0003$). Red:far-red ratios in the RV province were also significantly higher than those in the AP province ($F = 35.3$, $P < 0.0001$). The AP sites generally exhibited higher soil fertility than the RV sites with significantly higher values of K ($F = 8.6$, $P = 0.01$), Mg ($F = 9.2$, $P = 0.007$), percent organic matter ($F = 8.7$, $P = 0.009$), and CEC ($F = 16.8$, $P = 0.0007$), but lower values of C:N ($F = 26.1$, $P < 0.0001$). The Ca:Al was also higher for the AP sites but not significant. Litter depths were shallower and soil temperatures were higher on the RV sites than the AP sites, but neither were significant. The AP province had significantly greater herb ($F = 11.4$, $P = 0.003$), tree seedling ($F = 24.8$, $P < 0.0001$), and sapling richness ($F = 18.0$, $P = 0.0008$) than the RV province. The AP province had significantly more saplings ($F = 29.4$, $P < 0.0001$) than the RV province, while the RV province had significantly higher standing dead tree richness ($F = 8.0$, $P = 0.01$) and density ($F = 4.7$, $P = 0.04$) than the AP province (Appendix 1).

NE aspects had significantly deeper litter than the SW aspects ($F = 8.4$, $P = 0.01$), but SW aspects had higher soil temperature, though not significant. The NE-facing slopes had significantly higher values of K ($F = 5.9$, $P = 0.03$), Mg ($F = 11.0$, $P = 0.004$), Mn ($F = 25.5$, $P < 0.0001$), Ca:Al ($F = 13.1$, $P = 0.002$), CEC ($F = 10.9$, $P = 0.004$), and soil pH ($F = 13.1$; $P = 0.002$) but lower values of C:N

(F = 24.7, P < 0.0001), Fe (F = 19.0, P = 0.0004), and Zn (F = 4.5, P = 0.05) than the SW-facing slopes, suggesting higher soil fertility for the NE-facing slopes (Appendix 1).

There was a significant interaction between province and aspect for K (F = 5.32, P = 0.03) and Mg (F = 4.3, P = 0.05), with the NE-aspect sites in the AP province having higher concentrations of these soil nutrients than SW-aspect sites in the AP province, and sites on either aspect in the RV province. All possible interactions (province and aspect (F = 11.7, P = 0.003), province and management regime (F = 5.3, P = 0.005), aspect and management regime (F = 5.0, P = 0.007), and all three (F = 3.8, P = 0.02)) were significant for CEC. The combined comparisons showed that AP sites on NE slopes within the repeat burns had the highest CEC values. The pH range was narrow (between 4.2 and 4.6), and there was a significant interaction (F = 3.7, P = 0.02) among province, aspect and management regime as well as just between province and management regime (F = 2.9, P = 0.05) with AP, NE, and repeat burn sites having the highest pH. These interactions indicate that the NE slopes in the AP province have the highest soil fertility. We place lower confidence in the results that repeat burns on NE aspects and in the AP province were the most fertile because there was only one NE-facing, repeat burn site in the AP. There was a significant interaction between province and aspect for tree seedling richness, with AP province sites on SW slopes having significantly higher richness values than RV province sites on both SW and NE slopes (Fig. 3).

3.2. Germination rates

All three invasive species had very low germination rates (< 3%) in the control sites and both *AiAl* and *MiVi* showed significant differences among the five management regimes with the highest germination in the shelterwood sites. For *AiAl*, the control sites showed significantly lower germination rates than the DLC (Z = -2.98, p = 0.024) and shelterwood (Z = −4.27, P = 0.0002) sites, and the repeat burn (Z = −3.33, P = 0.0076) and single burn (Z = −3.84, P = 0.0011) sites showed lower germination rates than the shelterwood sites. *MiVi* germination rates were significantly lower for the control, single burn, repeat burn, and DLC sites compared with the shelterwood sites (Z = −3.23, P = 0.011). None of the management regimes differed in terms of germination rate for *AlPe*. All three species had higher rates of germination in the RV than the AP, but only *MiVi* was significant (χ^2 = 21.94, P < 0.0001). Germination rates were also higher on NE slopes than SW slopes, but only *AlPe* was significant (χ^2 = 5.89, P = 0.015) (Fig. 4).

3.3. Survival

Using the latest growing season measurements of the transplants, none of the three invasive plant species or *QuRu* differed significantly in seedling survival in terms of management regime or aspect. *AlPe* had a significantly higher survival rate in the AP province than the RV province, but *AiAl* and *MiVi* did not differ significantly by province. In contrast, *QuRu*, survived significantly better in the RV province than the AP province. The rate of survival decreased significantly from five weeks prior for *QuRu* (F = 28.5, P < 0.0001), *AiAl* (F = 25.8; P < 0.0001), and *AlPe* (F = 68.6; P < 0.0001). *AlPe*'s survival rate was the lowest of all four species. Due to *AlPe*'s low survival rate, subsequent measures of growth could only be based on 33 sites, and most of the excluded sites were the unmanaged control sites. *MiVi* did not show a significant difference in survival between the early and late season measures (Table 1 and Fig. 5). Differences in early and late-

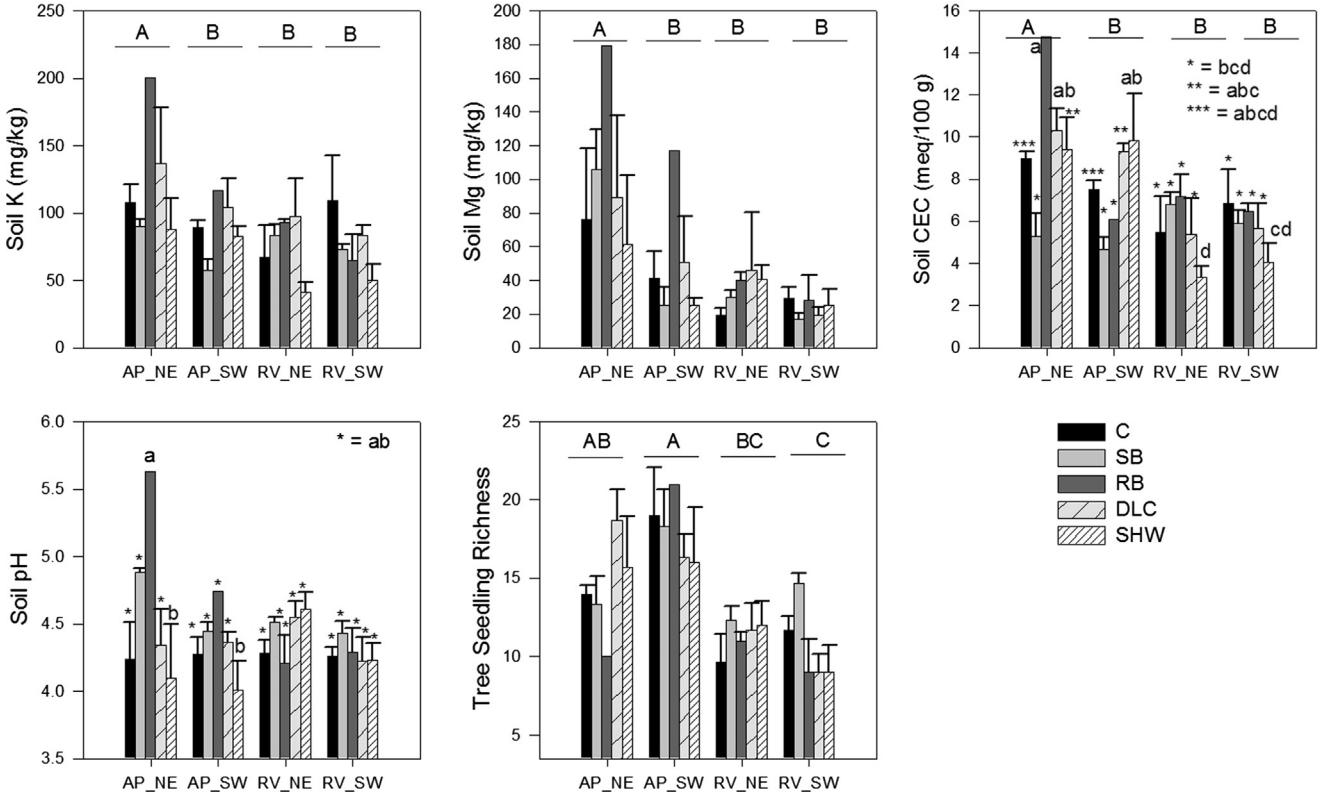

Fig. 3. Combined province and aspect interaction effects. Bar graphs show the means and standard errors of combined province and aspect interaction effects (X-axis) by the management regime effect (legend, where C = control, SB = single burn, RB = repeat burn, DLC = diameter limit cut, and SHW = shelterwood) for variables with significant interactions among these effects (K, Mg, CEC, pH, and tree seedling richness). Statistical comparisons were made using generalize linear mixed models. Upper case letters show significant differences between the combined province and aspect interaction, while smaller case letters show significant differences between the management types within each combined province and aspect interaction. Three asterix levels represent lower-case letter groupings that cannot be shown due to the narrow bars; these are defined in a legend within each graph.

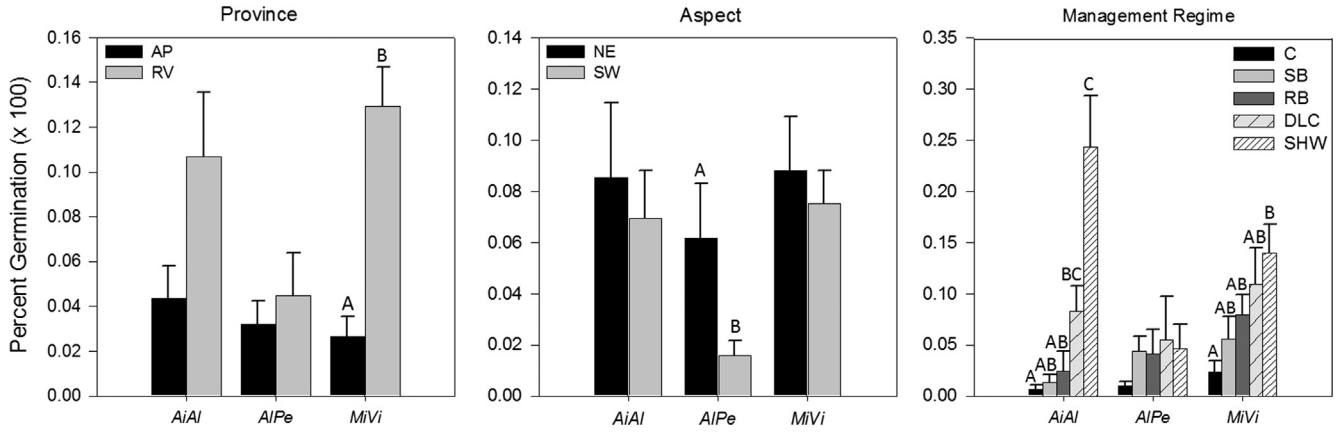

Fig. 4. Germination. Percent germination of the three invasive plants by province, aspect, and management regime. Statistical comparisons were made using a generalized linear mixed model. Comparisons within each category that have a different letter are significant, P-value of 0.05.

season survival was most evident for *AiAl* and *QuRu* compared to *AlPe* and *MiVi*, but with no significant difference between province or aspect or among management regimes, though *QuRu* showed less difference over the growing season in the harvested sites (Fig. 5).

3.4. Growth

AlPe shoot biomass was greater in the shelterwood sites than the DLC and control sites. Shoot height, number of leaves per tallest tiller, and shoot biomass of *MiVi* were all significantly greater in the shelterwood management regime compared with the control, single burn, and repeat burn sites. *AiAl* did not differ significantly in terms of number of leaves per main stem, shoot height, shoot or root biomass across the five management regimes, but root biomass was evidently lowest in the control sites. *QuRu* also did not differ significantly in terms of growth variables across the management regimes (Table 1, Figs. 6 and 7).

AlPe growth did not differ significantly between the AP and RV provinces. *AiAl* had significantly more leaves per main or dominant stem in the AP sites than in the RV sites, but was not taller and did not have a larger shoot biomass when comparing the two provinces. However, there was significantly greater root biomass in the RV province than the AP province for *AiAl.* Shoot height, number of leaves per tallest tiller, and shoot biomass of *MiVi* were all significantly greater in the RV province than the AP province. *QuRu* showed significantly greater shoot heights (F = 8.6, P = 0.02) in the AP province than the RV province (Table 1, Figs. 6 and 7).

AlPe shoot biomass was significantly greater on NE aspects than SW aspects. *AiAl* did not differ in terms of number of leaves per main stem, shoot height, or shoot biomass for aspect. There were significantly more *MiVi* leaves per tallest tiller on NE aspects compared to SW aspects. *QuRu* showed no significant differences in shoot height or stem diameter in terms of aspect (Table 1, Figs. 6 and 7).

There was a significant interaction between management regime and aspect (F = 4.1, P = 0.01) for *MiVi's* shoot biomass with plants on NE slopes in shelterwoods showing larger biomass than all other aspect and management combinations except SW slopes in shelterwoods and NE slopes in DLC stands (Fig. 8).

3.5. Herbivory

AiAl and *AlPe* showed no difference in general herbivory in terms of management regime, province, or aspect. *QuRu* also showed no significant differences in terms of general herbivory (deer and insect) for management regime, province, or aspect, but did show a significant difference in deer herbivory alone by management regime (F = 21.6, P = 0.0001) and province (F = 41.4, P = 0.0001). The DLC management regime and RV province had significantly higher amounts of deer herbivory than the other management regimes and the AP province, respectively (Fig. 8). In contrast, *MiVi* had significantly higher herbivory in the AP province than the RV province (Table 1 and Fig. 9).

For *MiVi,* there was a significant interaction between management regime and province (F = 3.2, P = 0.04), with AP province sites in repeat burns, single burns and control sites having significantly more herbivory than RV province sites in the single burn sites. For *QuRu*, there was a significant interaction between management regime and province (F = 15.0, P = 0.0005), with DLC sites in the RV province having more deer herbivory than all other province and management

Table 1
Percent survival and growth (shoot height, leaf number, and biomass) comparisons by species using a generalized linear mixed model (GLIMMIX), showing the F-value and the P-value (in parentheses). Number of leaves were determined using the main or dominant stem for *AiAl*, a total count of all basal leaves for *AlPe*, and the tallest or longest tiller for *MiVi. AiAl = Ailanthus altissima*, *AlPe = Alliaria petiolata*, and *MiVi = Microstegium vimineum*. C = control; DLC = diameter limit cut; SHW = shelterwood; SB = single burn. N used for the productivity measures includes only sites with surviving individuals and these values were 56, 33, and 56 for *AiAl*, *AlPe*, and *MiVi*, respectively. Root biomass was only measured for *AiAl*; NA = not applicable. Significant (P ≤ 0.05) results are in bold. Any variables showing significant interactions among the categories (Province, Aspect, or Management Regime) are marked with an * and these are described in the text and presented in Fig. 8. Values for *QuRu* are in the text.

	Province			Aspect			Management Regime		
	AiAl	*AlPe*	*MiVi*	*AiAl*	*AlPe*	*MiVi*	*AiAl*	*AlPe*	*MiVi*
Percent Survival	0.7 (0.4)	4.5 (0.05)	1.0 (0.3)	0.3 (0.7)	1.1 (0.3)	0.9 (0.3)	0.3 (0.9)	1.8 (0.2)	0.9 (0.5)
Shoot Height	3.8 (0.07)	22.6 (0.1)	**4.7 (0.05)**	0.8 (0.4)	2.2 (0.4)	0.03 (0.9)	1.7 (0.2)	11.9 (0.2)	**7.7 (0.0009)**
Number of Leaves	**16.7 (0.0007)**	0.04 (0.9)	**6.3 (0.02)**	0.3 (0.6)	3.2 (0.3)	**6.1 (0.02)**	1.1 (0.4)	0.3 (0.9)	**8.5 (0.0005)**
Shoot Biomass*	0.1 (0.7)	2.0 (0.3)	**9.2 (0.007)**	0.1 (0.7)	**21.1 (0.04)**	3.0 (0.1)	1.0 (0.5)	**19.7 (0.05)**	**8.7 (0.0004)**
Root Biomass	**14.9 (0.001)**	NA	NA	1.5 (0.2)	NA	NA	1.4 (0.3)	NA	NA
Herbivory*	2.8 (0.1)	0.8 (0.5)	**25.8 (0.0001)**	0.7 (0.4)	28.2 (0.1)	3.1 (0.10)	0.9 (0.5)	1.0 (0.6)	1.3 (0.3)

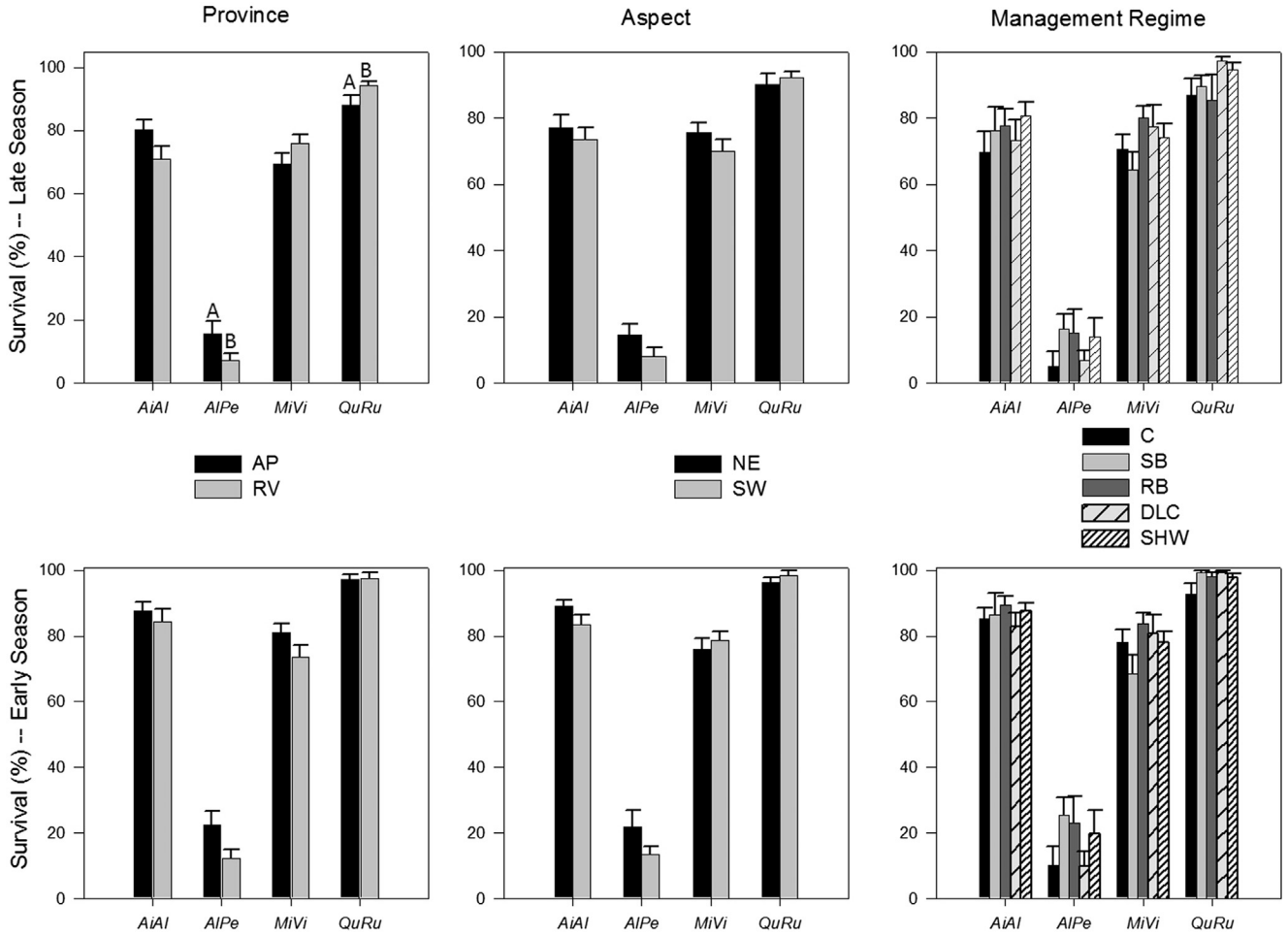

Fig. 5. Survival. Percent survival of transplants and increase in mortality between two measurements in the growing season for the three invasive plants and oak by province, aspect, and management regime. Statistical comparisons were made using a generalized linear mixed model. Comparisons within each category that have a different letter are significant, P-value of 0.05.

regime combinations (Fig. 8). We suspected this was due to one DLC site in the RV province on which the owner often fed the deer. However, after removing this site from the analyses, the same significant pattern occurred.

We evaluated the effects of deer herbivory on *QuRu* further by separating out the fenced and unfenced plots. None of the five management regimes showed significant differences in *QuRu* growth between fenced or unfenced plots, though *QuRu* stems tended to be taller in the fenced plots for each. Fenced plots tended to have a greater change in stem diameter than the unfenced plots when comparing by management regime, province, and aspect, but none were significant. *QuRu* in the RV province had significantly taller stems in fenced plots than the unfenced plots, but this trend was not significant for *QuRu* in the AP province (Table 2 and Fig. 9). *QuRu* in fenced plots on NE-facing slopes and SW-facing slopes both had significantly taller stems than oaks in unfenced plots (Table 2 and Fig. 10).

4. Discussion

Use of different harvesting techniques and prescribed burns to open forest canopies may promote both native species regeneration as well as invasion by nonnative invasive plants. The effectiveness of these management strategies on native species regeneration varies with existing regional site conditions (physiographic province) and local topography (slope aspect). Logically invasive plants' success in different management regimes should also vary by local and regional physiographic site conditions. In this study, we evaluated how *MiVi, AlPe*, and *AiAl* responded to shelterwood and diameter-limit cut harvests and fires of different frequencies in terms of their ability to germinate, survive, and grow relative to the native *QuRu* across two different provinces and two different aspects. Our goal was to provide potential management strategies that reduce the risk of invasion in response to forest management by manipulating disturbance severity or selecting particular site conditions.

4.1. Site conditions and native vegetation patterns of the management regimes, provinces, and aspects

Though canopy opening for the shelterwood sites is twice as large as for the DLC sites, the red-far red ratios do not show this distinction likely due to understory growth at and just above the 1-m height at which both the photographs and light measures were taken. Shelterwoods have more total herb, shrub, and vine cover (much of this *Rubus* spp. in some sites) than the other management regimes, including the DLC sites. Canopy opening differences between the two provinces may be attributed to the AP (less canopy opening) having more saplings and fewer standing dead trees than the RV (more canopy opening). Higher levels of soil fertility variables in the AP and NE aspect sites may partially explain the higher native species diversity values, higher sapling densities, and herb cover at these same sites. The RV province sites appear to be of relative low productivity which is reflected in the species composition (Huebner and McGill, 2018).

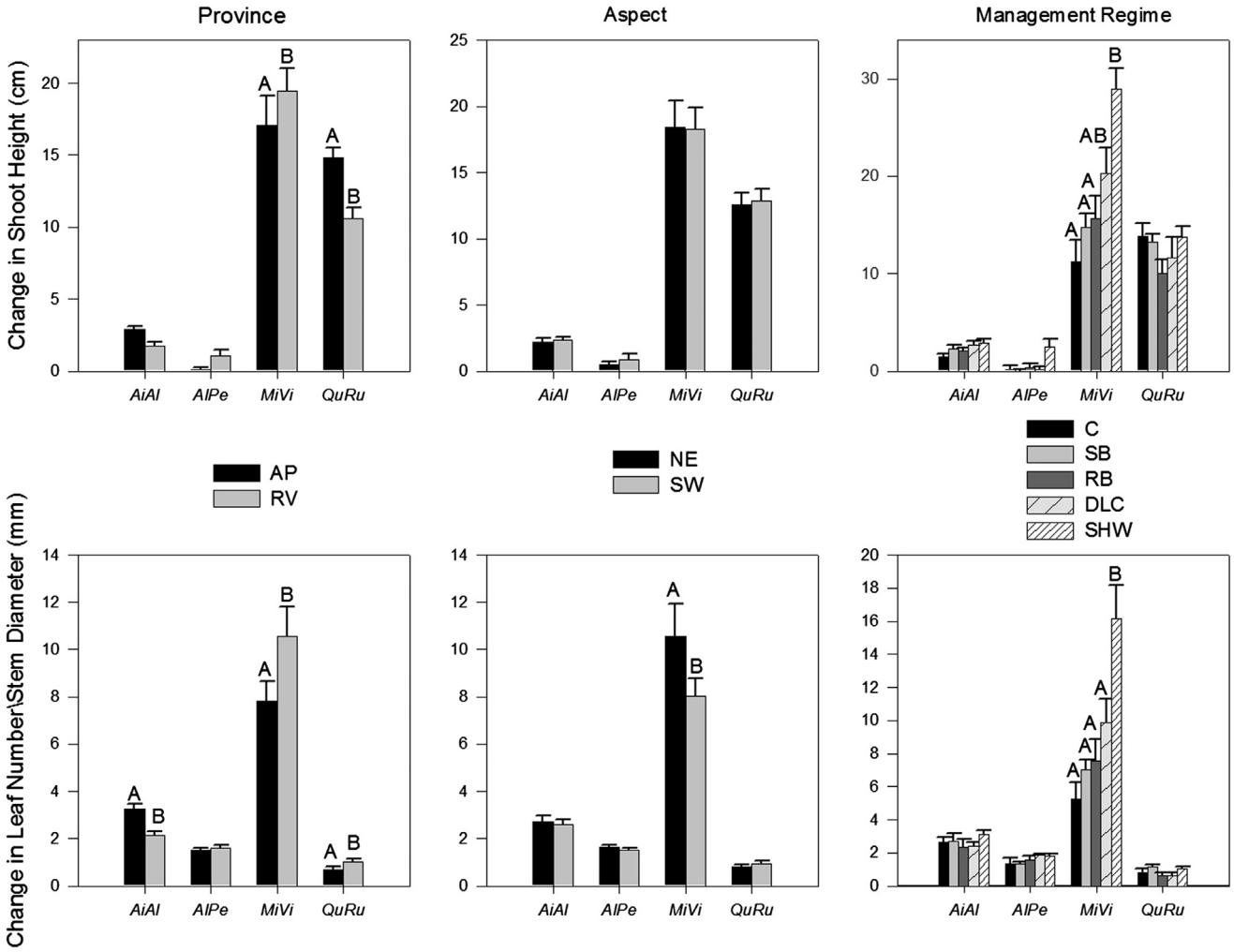

Fig. 6. Growth. Change in shoot height (all three invasive plants and *QuRu*), leaf number (the three invasive plants), and stem diameter (the oak) by province, aspect, and management regime. Statistical comparisons were made using a generalized linear mixed model. Comparisons within each category that have a different letter are significant, P-value of 0.05.

4.2. Germination

A lack of disturbance ensures low levels of germination for all three invasive species, whereas, high levels of disturbance as associated with shelterwood harvests support the highest germination rates for all three invasive species, though not statistically significant for *AlPe*. The higher germination rates for all three invasive plants in the RV province and NE aspects suggests these landscapes may be more vulnerable to early establishment of invasive plants when there is a seed source. The higher soil moisture (not directly measured) associated with NE aspects as well as the greater canopy opening associated with the RV province may play a role in the germination success for all three invasive plants addressed in this study. Based on these findings, we conclude that these invasive species are more likely to germinate under conditions of greater canopy opening (RV and shelterwood and DLC harvests) provided there is sufficient soil moisture (NE aspects). However, all three species are capable of germinating at high percentages (above 80%) under controlled laboratory conditions in complete darkness under ideal day/night temperature cycles (Huebner, Pers. Obs.), suggesting that other factors, such as soil temperature, may play a role.

In general, the highest germination rates that we found (about 15, 5, and 25% for *MiVi*, *AlPe*, and *AiAl*, respectively) were lower than those found in the literature under similar conditions (30% for *MiVi* (Schramm and Ehrenfeld, 2010), 5–9% for *AlPe* (Cavers et al., 1979), and 45% for *AiAl* (Kota et al., 2007). Germination rates of *AiAl* and *MiVi* may have been even lower if we had planted them in the fall and let them overwinter in the field as was necessary for *AlPe* (making them more vulnerable to predators and pathogens), instead of using the refrigerator to mimic an overwintering period. Indeed, *MiVi* shows signs of being susceptible to mortality in the soil, but the same is not true for *AlPe* (Redwood et al., 2018). However, surviving seed of *MiVi* buried in mesh bags in the soil have germination rates between 86 and 89% after one and two years (Redwood et al., 2018). *AiAl* shows similar protection from soil mortality as *AlPe* (Huebner, Pers. Obs.). The germination rates in our study reflect not only a response to the environmental conditions but also potential seed dormancy (all three species) and mortality (potentially highest for *MiVi*). The relatively low germination rate manifested suggests that the germination stage is sensitive to stochastic events for *MiVi*, *AlPe*, and *AiAl*. However, our results show that sites with any type of canopy opening, especially a timber harvest, and sites in the RV province and on NE aspects are more vulnerable to germination of these three invasive plants than undisturbed, AP province, and SW aspect sites. Moreover, oak acorn removal greater than 90% can be expected in the field (Garcia and Houle, 2005). Such removal may be primarily by rodents (Garcia and Houle, 2005), but deer can also remove a significant portion of unburied acorns (García et al., 2002). Because of high seed predation, acorns are likely to have lower germination rates than the those associated with these three nonnative plants, except possibly in mast years due to rodent caching (Crow, 1988) in which the buried acorns may have germination rates as high as

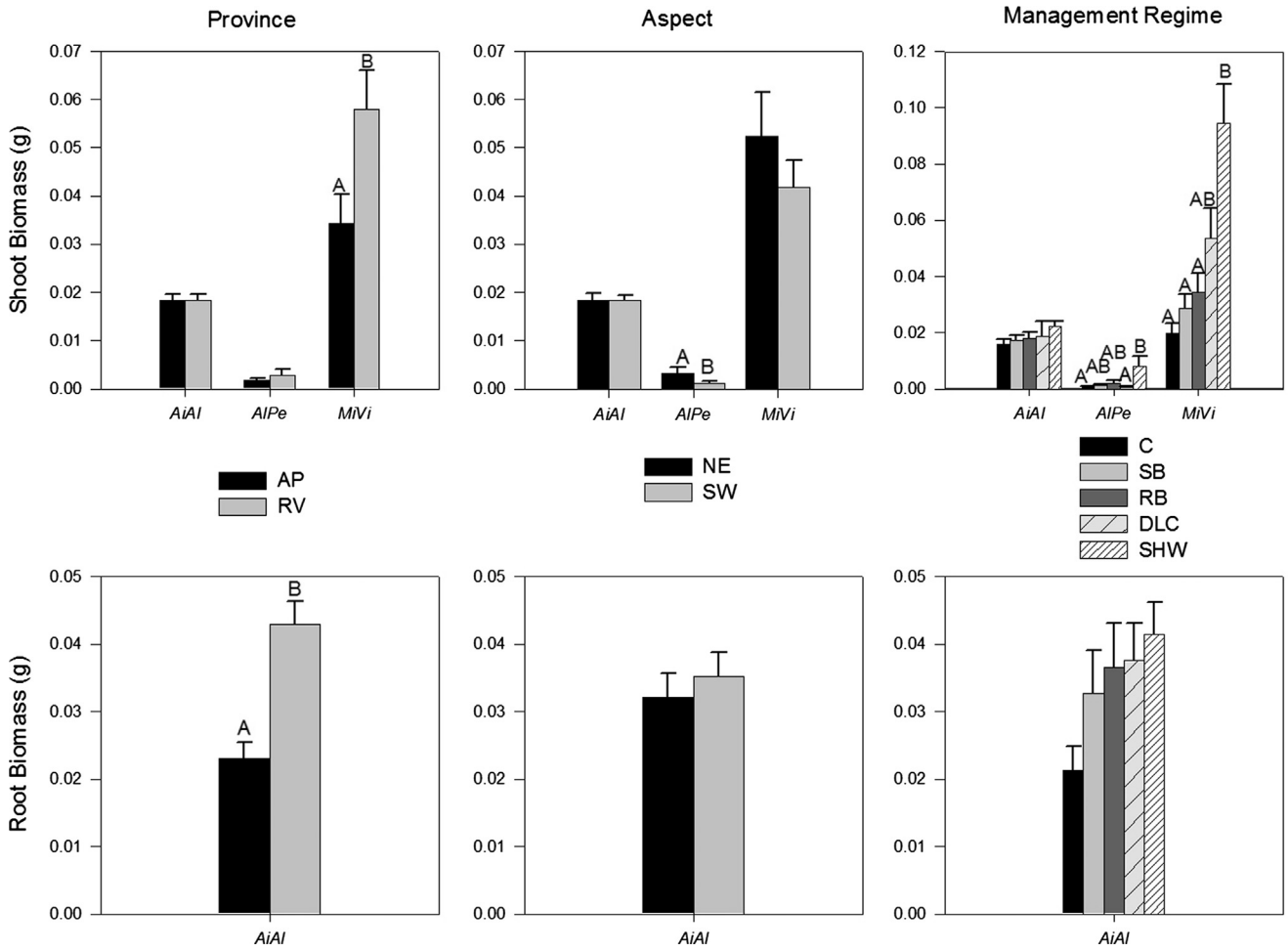

Fig. 7. Biomass. Shoot (all three invasive plants) and root biomass (*AiAl*) by province, aspect, and management regime. Statistical comparisons were made using a generalized linear mixed model. Comparisons within each category that have a different letter are significant, P-value of 0.05.

92% (García et al., 2002).

In our study, only seed from the same province of each site were used, indicating that RV seed may germinate better in RV sites than AP seed at AP sites. Genetic differences between populations from these provinces (Culley et al., 2016) may in part explain the differences in germination for *MiVi*. Existing genetic variation among populations of *AlPe* (Byers and Quinn, 1998; Meekins et al., 2001) and *AiAl* (Aldrich et al., 2010) could lead us to expect higher germination rates for seed collected from the province within which it is planted. However, we cannot provide an explanation related to seed fitness for why RV seed would germinate better than AP seed, other than the RV province tends to have less litter and higher soil temperatures.

Because we first evaluated germination five weeks after planting, there may be some early deaths that decomposed before the first tallies.

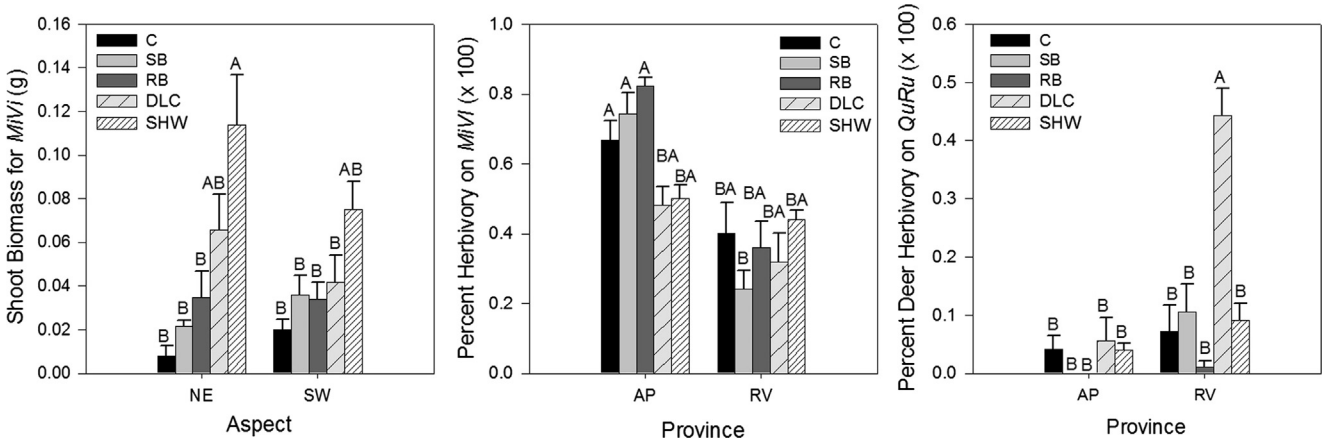

Fig. 8. Interactions for shoot biomass and herbivory. *MiVi* shoot biomass had a significant aspect and management interaction; *MiVi* herbivory also had a significant province and management regime interaction; *QuRu* deer herbivory had a significant province and management regime interaction. These interactions were fixed effects in generalized linear mixed models. Comparisons that have a different letter are significant, P-value of 0.05.

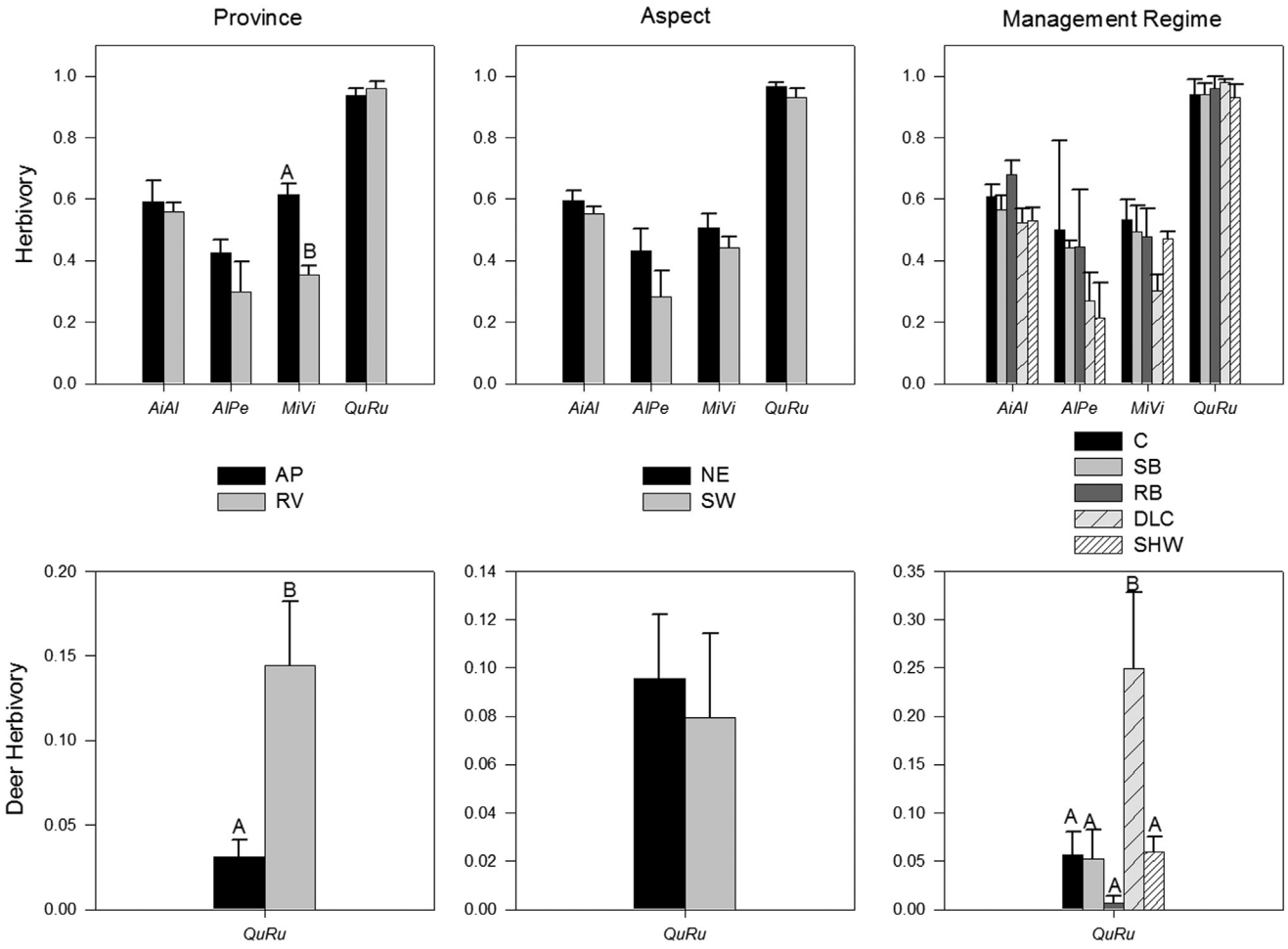

Fig. 9. Herbivory. Presence of invertebrate herbivory of three invasive plants (deer herbivory was documented for the invasive plants) and both invertebrate and deer herbivory for *QuRu* by province, aspect, and management regime. Statistical comparisons were made using a generalized linear mixed model. Comparisons within each category that have a different letter are significant, P-value of 0.05. Deer herbivory estimates for *QuRu* are based on the combined fenced and unfenced plots.

Also, some seeds may germinate but fail to grow through the soil and litter, a circumstance that has been supported by other studies for *MiVi* (Oswalt and Oswalt, 2007; Schramm and Ehrenfeld, 2010), *AlPe* (Cavers et al., 1979), and *AiAl* (Kostel-Hughes et al., 2005). Most of these germinants from the first tally survived to the second tally five weeks later (no significant difference between the two tallies), suggesting that once a germinant is able to grow beyond the soil and litter layers, it is likely to survive for further growth.

4.3. Survival

AlPe had the lowest survival of the three nonnative plants and *QuRu*, possibly caused by being transplanted at an earlier life stage than the others. None of the three invasive plants nor *QuRu* differ significantly in survival across the five management regimes, suggesting that *AiAl* is similar to *QuRu*, which can build up seedling banks (Frey et al., 2007; Arthur et al., 2012). Such seedling banks may enable the species to wait and respond to more favorable conditions at which point they experience a growth spurt. Such conditions would have to occur within a single growing season for *MiVi*, hence the importance of also having a seed bank and being shade-tolerant. This annual grass is capable of reproducing under closed-canopy conditions, though seed may be fewer in number and lower in quality than seed produced by plants grown under higher light conditions (Cheplick 2005; Huebner, 2011).

AlPe is shade-tolerant as a rosette and more likely to survive at greater abundance in shadier environments (Phillips-Mao et al., 2014) as is associated with the AP province compared to the more open forests of RV province. Our results, which show greater survivorship of *AlPe* in the AP province, support this. Based on Phillips-Mao et al. (2014) findings, we may predict *AlPe*'s survival into the second year, when it

Table 2
Shoot height and stem diameter comparisons for *QuRu* in fenced vs. unfenced plots using a generalized linear mixed model (GLIMMIX), showing the F-value and the P-value (in parentheses). C = control; DLC = diameter limit cut; RB = repeat burn; SHW = shelterwood; SB = single burn. N used for the productivity measures includes only sites with surviving individuals (20). Significant (P ≤ 0.05) results are in bold.

	Province		Aspect		Management Regime				
	AP	RV	NE	SW	C	SB	RB	DLC	SHW
Shoot Height	2.6 (0.1)	**12.2 (0.002)**	**5.1 (0.04)**	**6.3 (0.02)**	3.5 (0.09)	2.5 (0.1)	4.5 (0.07)	4.3 (0.06)	0.01 (0.9)
Stem Diameter	3.5 (0.07)	0.9 (0.4)	1.5 (0.2)	2.3 (0.1)	0.1 (0.7)	0.4 (0.5)	0.3 (0.6)	4.2 (0.07)	1.4 (0.3)

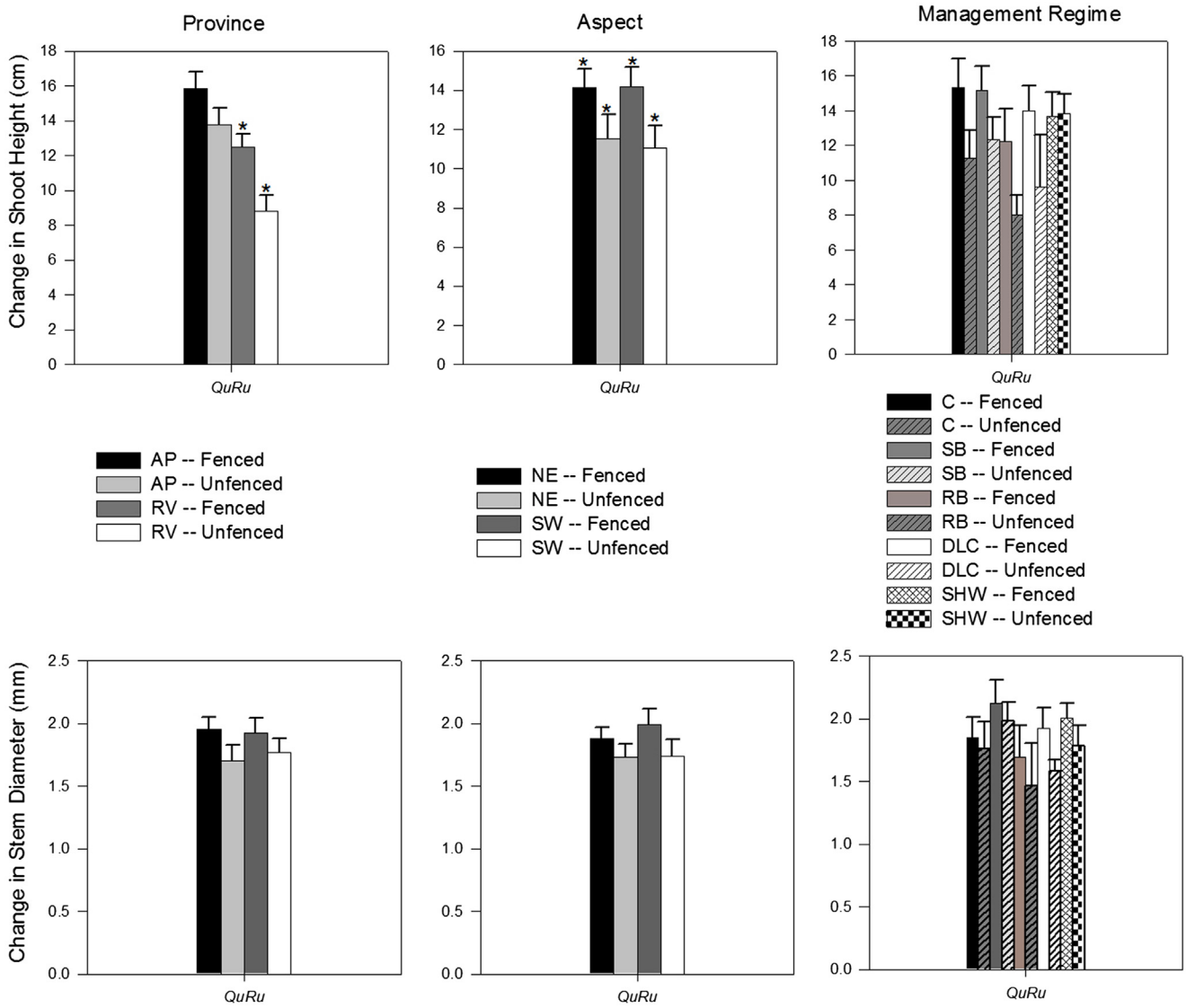

Fig. 10. Fenced vs. unfenced plots. Change in shoot height and stem diameter for *QuRu*, comparing fenced and unfenced plots by the categories: province, aspect, and management regime. Statistical comparisons were made using a generalized linear mixed model. Comparisons between fenced and unfenced plots that have an * are significant, P-value of 0.05.

flowers, to be as high or higher in the RV province than the AP province as well as higher in the disturbed management regimes because as planted in our study, each individual plant is likely to put more energy into its own growth under higher light conditions (Phillips-Mao et al., 2014). However, if these high light sites were to become invaded with several stems of *AlPe*, it is likely, based on Phillips-Mao et al.'s research, there would be lower overall survival, though the few surviving would be more productive. Our results show that *QuRu* has greater survival in the RV province, possibly giving it a small advantage over *AlPe* in these drier sites at least during *AlPe*'s first year of growth. Unfortunately, *MiVi* and *AiAl* show no significant difference in survival by province and *MiVi* may also show a tendency to survive better in the RV province.

AiAl has been documented to survive as clonal ramets under closed forest canopies as long as 19 years with very slow growth rates, though seedling mortality under these same conditions is 100% (Kowarik, 1995). In contrast, Knűsel et al. (2017) shows greater survival of seedlings than vegetative sprouts in high-shade environments. Our results agree with Knűsel et al. (2017), in part, because we show 70–80% survival of young *AiAl* seedlings under all management regimes, including the undisturbed closed canopy forests. Kowarik (1995) hypothesized that *AiAl* ramets are in a semi-dormant state when in the shade, but Hamerlynck (2001) concludes *AiAl* shade ramets are actively photosynthesizing and have the ability to couple shade-plant like photosynthetic efficiency with the high photosynthetic capacity under full-sun conditions. *AiAl* is also capable of optimizing water-use efficiency under both full-sun and shaded conditions (Hamerlynck, 2001).

It is important to keep in mind that our survival rates are based on only one growing season. Kota et al. (2007) show survival rates between 3 and 15% under closed canopies but up to 35% and 40% in clear cut and selectively cut forests, respectively, for *AiAl* after two growing seasons. Martin et al. (2010) show *AiAl* survival rates over five years of 22% and 37% at light levels similar to levels found in closed canopy forests and burn sites, respectively, and 55% at light levels similar to levels found in our DLC sites.

Our *QuRu* transplants show similar survival rates as those found by Martin et al. (2010) and Dey and Parker (1997a) in closed-canopy sites but about 10% lower survival than that found in both Martin et al., (2010) DLC-like light conditions and Dey and Parker's (1997a) shelterwood conditions. Martin et al.'s survival values are based on saplings taller than 1.4 m in height, which likely experience less deer browse and may be less susceptible in general to any stressful environmental

conditions. Also, Dey and Parker's (1997a) paper did not mention deer impacts and, thus, it may not be an issue at their sites. Similarly, Morrissey et al. (2010) planted *QuRu* stock over a gradient of forest canopy gap and found a range 35 – 65% survival with larger gap openings (about 0.4 ha) having greater survival. Morrissey et al. (2010) planted trees were not protected by deer (half our plant oaks were protected), which may explain the lower survival rates. *QuRu* is planted as an older seedling in our study and, consequently, is more likely to survive than if it were planted as a new germinant but less than that of a taller sapling. Though our data do not allow us to model long-term survival, our findings show similar rates of survival/mortality under similar management regimes found in the literature. More importantly, with some protection from deer, planted *QuRu* seedlings could potentially survive just as well as *MiVi* and better than *AiAl* and *AlPe* in similar management regimes.

4.4. Growth

Because of the apparent vulnerability to mortality of these three nonnative species at the germination and seedling stages, especially *AlPe* and *AiAl*, we may expect the success of these nonnative invasive species to be explained by high growth rates relative to associated native species, such as *QuRu.* In our study, both *MiVi* and *AlPe* show increased growth and greater productivity in the most disturbed management regimes (shelterwoods) and on NE aspects. Further, compared to *AlPe* or *AiAl, MiVi* appears to grow larger with more leaves in the more open RV province than the AP province. These patterns of growth for *AlPe* and *MiVi* follow the patterns associated with their successful germination rates. Thus, as long as water is not limiting, early-establishing *MiVi* and *AlPe* that survive are most likely to grow best in more exposed or disturbed sites. The positive association of *MiVi* and *AlPe* growth with higher levels of light is well-established in the literature. *MiVi* plants grow larger in response to higher light levels, though light values above 25% full sunlight are wasted (Winter et al., 1982; Horton and Neufeld, 1998; Huebner, 2011; Glasgow and Matlack, 2007; Cheplick and Fox, 2011); these larger plants also produce more seed than the smaller plants grown under lower light conditions (Huebner, 2011; Cheplick and Fox, 2011). Similarly, *AlPe,* puts more energy into producing fewer larger, productive flowering plants, under higher light conditions (Phillips-Mao et al., 2014). Our study shows that *AlPe* starts to focus its energy into growth when under higher light and conditions during its first year of growth, though the reduction in individual plant density is not likely to take place until the second year (Phillips-Mao et al., 2014).

In contrast, *AiAl* shows no difference in above-ground growth for the first growing season in terms of management regime, province, or aspect. However, *AiAl* shows significantly greater root biomass in the RV province with evident greater root biomass associated with plants on SW aspects and the burn and harvest sites. These results suggest *AiAl* is allocating most of its energy to root system development, at least for the first year and can do so best in higher light environments. However, *AiAl* can respond rapidly to intermittent increases in light Knapp and Canham (2000), and rapid growth may be essential for *AiAl* due to poor survival in low-light environments (Martin et al., 2010). Thus, based on our results, we propose that *AiAl* can tolerate shade conditions and respond rapidly to high light conditions only after adequate development of its root system. Our results show that one growing season may not be enough time for the root system to develop, which could potentially give land managers time to respond to new *AiAl* invasions starting from seed. We could not allow *AiAl* to grow for additional growing seasons because of its ability to sprout even from root fragments as small as 2 cm in length (Huebner, Pers. Obs.) though 3–6 cm fragments may ensure greater success (Del Tredici, 1995). A larger root system would be difficult to remove with certainty. More research is needed to determine how fast the *AiAl* root system develops under different light and soil conditions.

QuRu's relative increase in growth on the RV sites compared to AP sites is similar to other studies that argue for decreased native understory competition as the primary factor leading to *QuRu* success on poor sites with lower site indices (Schlesinger et al., 1993; Spetich et al., 2002; Morrissey et al., 2010: Major et al., 2013; Waller and Maas, 2013). *QuRu* also has proven to be a poor competitor against some nonnative species (Meekins and McCarthy, 1999; Marshall et al., 2009; Beasley and McCarthy, 2011). In our study, *QuRu*'s change in shoot growth is greater than that of *AiAl* and *AlPe*. Given that the oak seedlings are already a year old with more root development than the invasive species transplants, *QuRu*'s larger change in shoot growth compare to that of *AiAl* and *AlPe* is not surprising. Although, our *QuRu* stock is from both RV and AP sources, we were unable to transplant province-specific stock in each province, and there is a chance most of the stock is from AP given the larger extent of this province. Nonetheless, these data provide support for the use of artificial regeneration in sites where natural regeneration is unlikely and invasion by exotics is highly probable. Poor natural oak regeneration is not only attributed to a lack of canopy opening and light (Brose et al., 1999a; 1999b), but also the depletion of native seed, seedling banks, and saplings often the result of long-term deer herbivory (Nuttle et al., 2014). Our data show that deer herbivory impacts shoot height but does not impact stem diameter as much as regional physiography. Stem diameter, normally a good correlate of stem height without deer herbivory, also is a good correlate of root development (Dey and Parker, 1997b). Although mortality within one growing season in our study is much higher for the control and burn sites than the harvested sites, growth does not differ among the management regimes for those *QuRu* seedlings that survive. However, another year of growth shows a significant relationship between diameter growth and higher light levels (Regula, 2013), which is supported by many other studies that show a need for increased light to ensure oak regeneration (Larsen et al., 1997; Miller et al., 2006; Paquette et al., 2006; Dech et al., 2008; Dey et al., 2012).

Exactly how much additional light is needed for oak regeneration depends on site quality and how much of an oak component is desired (Schlesinger 1993). Determining the ideal light level that provides enough oak regeneration but does not promote growth of exotic species is critical when trying to prevent invasion by exotic plants. Canopy openings below those corresponding to the DLC-type harvests of our study (about 15%), would prevent increases in productivity of many shorter-lived invasive plants, such as *MiVi* and *AlPe*. If canopy opening levels can be kept below this DLC level for at least a year and possibly longer, increased growth of longer-lived invasive plants, such as *AiAl*, may be deterred. The presence and density of *AiAl* seedlings has been positively associated with harvest history, but not with fire (Rebbeck et al., 2017), which agrees with our findings of higher germination rates in the harvested sites. However, the fact that our study shows an increase in root growth for *AiAl* for canopy openings after burns as well as DLC and shelterwood harvests suggests the seedlings in burn sites may also eventually be able to rapidly respond to any increase in light, such as a canopy gaps due to a tree fall or death.

Other studies show that adequate oak regeneration is possible with less canopy opening. For instance, Schuler (2004) reveals that similar incremental diameter growth of *QuRu* is found for single-tree selection, DLC, or patch cuts. Also, Miller et al. (2017) concludes that oak regeneration does not differ between midstory removal (light levels below 200 μmol m^{-2} s^{-1}) and an overstory shelterwood (light levels below 500 μmol m^{-2} s^{-1}) provided the stands are fenced and herbicide is applied once to treat competing understory vegetation (fern, *Acer rubra*, *A. pennsylvanicum*, and *Fagus grandifolia* saplings less than 2-in dbh) within five years of the treatments. Applying herbicide more than one time may increase oak regeneration in the overstory shelterwood compared to the midstory removal (Miller et al., 2017), but doing so may also negatively affect other native species (Huebner et al., 2010). These same midstory removals with fencing result in the best restoration of native liliaceous understory species, and these liliaceous species

recover from the herbicide application in fenced areas under the midstory removals after six years (Huebner et al., 2010). Thus, it may be possible to reduce growth of at least three common invaders and still maintain oak regeneration. However, we may have to choose between (a) no herbicide treatment and early recovery of native understory species, which may serve as competitors against newly colonizing invasive plants, or (b) herbicide treatment with more oak regeneration but with delayed recovery of these understory species, and hope that invaders are not able to establish while native species are recovering from the herbicide. The difference between the midstory treatment with just fencing and with both fencing and herbicide is not significant in Miller et al. (2017) study, suggesting it may be worthwhile not to apply the herbicide and trade slightly less oak regeneration for recovery of a diverse native understory.

4.5. Herbivory

Our data show that all three invasive plants may suffer from invertebrate herbivory, which is supported by other studies showing both rapid adaptation of native herbivores to invasive plants (Siemann et al., 2006) and increased herbivory with increasing time since introduction of the invasive plant (Brändle et al., 2008), though this pattern is not universally true (Carpenter and Cappuccino, 2005). All three of our invasive species have documented herbivores, but we cannot be sure these are the ones that fed on our plants. *MiVi* has at least eight invertebrates known to feed on it (Bradford et al., 2010), *AlPe*, at least three (Yates and Murphy, 2008), and *AiAl*, at least 10 (Ding et al., 2006). Our findings support potential herbivore accumulation, similar to pathogen accumulation already documented for *MiVi* and *AiAl* (Flory and Clay, 2013). Though there is no evidence at our sites of the pathogens *Bipolaris* spp. (Kleczewaski and Flory, 2010) or *Verticillium nonalfalfae*. (Rebbeck et al., 2013; Snyder et al., 2013) known to attack and kill *MiVi* (differentially by species and location; Bruchart et al., 2017) and *AiAl*, respectively. There may also be environmental factors affecting the likelihood of herbivory or the degree of impact. For instance, temperature has been correlated with both increases and decreases in insect herbivory (Lemoine et al., 2014). The AP and NE aspect sites, which both had slightly lower soil temperatures than the RV and SW aspect sites in our study area, tended to have more general herbivory for all three invasive species. All in all, herbivory should be considered a significant factor in the lack of establishment success of these three invasive plants; however, their levels of herbivory are still far less than that experienced by *QuRu*.

4.6. Conclusions

Short-term studies such as this one (one growing season) may reflect current climatic conditions instead of a general pattern if the climate differs greatly from other years. Precipitation and drought indices show 2011 as wetter than normal compared to a 20th Century average for both provinces, but only in the top 1/3. Indeed, the month of July was drier than normal for both provinces in 2011 (National Climate Data Center). It is possible that being wetter than normal for the year may have increased competition by other plants in both provinces, and the relative drier and poor soil nutrient conditions of the RV and consequent lack of competition, made it easier for the exotics to germinate and grow.

The association between the RV province, which had lower plant species diversity, sapling density, herb cover, and soil fertility, and early establishment of *MiVi*, *AlPe*, and *AiAl*, suggests these species, like *QuRu,* are poor competitors on the most productive sites in their early stages of establishment. Other studies evaluating stand level patterns of invasion have shown a positive relationship between native species diversity and the presence of invasive plants that likely reflects the effect of environmental variables (e.g., light, soil fertility and moisture) that co-vary with species diversity (Stohlgren et al., 1999, 2003; Huebner and Tobin, 2006; Eschtruth and Battles, 2009). It is possible, the low germination (all three species) and slow growth (*AlPe* and *AiAl*) associated more with the more species-rich and fertile AP province are examples of resistance to invasion due to high plant diversity (Naeem et al., 2000). More likely, these species may benefit most from the larger canopy openings of the RV province sites and the higher soil fertility and soil moisture associated with NE aspects. Nonetheless, *QuRu*'s relative increase in growth on the RV sites compared to the AP sites is supported by other studies that argue for decreased competition as the primary factor leading to *QuRu* success on poor sites with lower site indices (Schlesinger et al., 1993; Spetich et al., 2002; Morrissey et al., 2010).

In agreement with Iannone et al. (2016) findings, our data also show that different invasive species do not share the same environmental preferences in terms of early establishment, especially if the species vary by habit (e.g., annual grass vs. biennial forb vs. tree). It is also important to distinguish between degree of invasion and vulnerability to invasion (Huston, 2004; Guo et al., 2015). Our findings may appear to disagree with Riitters et al. (2017) and Huebner's (2010) papers, which both show greater invasion of the AP province over the RV province. While our study focuses on site conditions associated with successful establishment of these three invasive plants, Riitters et al. (2017) and Huebner's (2010) studies focus on patterns of invaded sites and the degree of invasion. Thus, our results show that sites predicted to be the most vulnerable to early invasive plant establishment are not necessarily the most likely to have the highest degree of invasion.

MiVi, *AlPe*, and *AiAl* have become highly successful invaders of forests in spite of showing very low germination, high short-term mortality and low growth rates during their first growing season. It is apparent that these three invasive species share some characteristics with native species in that their survival and growth is initially precarious and dependent on adequate resources with minimal competition. Our findings show that all three species are most likely to have the highest germination rates (albeit low) on NE aspects in the RV province and are least likely to germinate in forests with closed canopies. The three species differ in terms of survival, with *AiAl* and *AlPe* showing higher survival in the AP province on NE aspects, whereas *MiVi* survives best in the RV province but also on NE aspects. Survival of none of the three differ by management regime, though mortality is lower in the shelterwoods for *MiVi* and *AiAl*. *MiVi* is the only species that shows any significant above-ground growth, with better growth occurring in the RV province, on NE aspects, and in shelterwoods. *AiAl*, however, has significant below-ground growth in the RV province. Thus, of these three invasive species, *MiVi* will be the first to visibly colonize a harvested site in the RV province, but *AiAl* is likely establishing its root system on these same sites and may be expected to produce more above-ground growth in subsequent years. However, precisely when more energy will be allocated toward shoot growth remains unknown. Because all three species experienced herbivory, and herbivory may be increasing since these species first were introduced to the US, it is possible that we are witnessing a decrease in survival and growth in part due to newly acquired enemies. However, this herbivory is still much lower than that affecting native species, such as *QuRu*.

We postulate that these three invasive species have become successful invaders primarily due to initial colonization of relatively poor sites, such as low-soil fertility sites with less competing vegetation (e.g., our RV sites), possibly including sites with depleted native seed and sprout banks. The increase in propagules of invasive plant species and the spread of these species is possible, in part, because such poor sites are relatively common. Management that focuses on sustainable, multiple native species regeneration should theoretically decrease the likelihood of establishment of these invasive species into uninvaded sites. While it may take *QuRu* 5–10 years to become established in high light conditions, *MiVi* can produce significant amounts of seed within one year. Nonetheless, keeping canopy openings under 15% and encouraging native understory competition with fencing or artificial

regeneration (seeding or transplants), where native sources are limited, could deter colonization of new sites by invasive plants and still promote regeneration of native species, such as oak.

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Appendix A

Means of light, soil, and species cover, richness, density and basal area variables. Numbers in parentheses are the standard errors. Numbers in bold are significantly different at $P \leq 0.05$ and means with different letters are significantly different within each category using a generalized linear mixed model. C = control; DLC = diameter limit cut; RB = repeat burn; SHW = shelterwood; SB = single burn. Units were measured in mg/kg for K, Mg, Mn, P, Fe, and Zn. H/S/V cover = total Herb, Shrub, and vine Cover.

	Province		Aspect		Management Regime				
	AP	RV	NE	SW	C	SB	RB	DLC	SHW
Canopy Opening (%)	**7.9a (1.0)**	**17.4b (3.0)**	12.7 (2.4)	13.4 (2.5)	**4.6a (0.006)**	**9.1ab (0.02)**	**6.9a (0.01)**	**14.4b (0.03)**	**28.1b (0.05)**
Red:Far-red	**0.3a (0.04)**	**0.6b (0.03)**	0.5 (0.05)	0.5 (0.03)	0.4 (0.06)	0.4 (0.07)	0.5 (0.09)	0.5 (0.06)	0.6 (0.05)
pH	4.40 (0.09)	4.36 (0.04)	**4.6a (0.08)**	**4.3b (0.05)**	**4.3a (0.07)**	**4.6ab (0.06)**	**4.5b (0.2)**	**4.4ab (0.08)**	**4.2ab (0.1)**
% Organic Matter	**8.32a (0.5)**	**6.17b (0.4)**	7.4 (0.5)	7.0 (0.5)	7.8 (0.9)	5.5 (0.2)	7.3 (0.8)	7.9 (0.7)	7.4 (1.0)
CEC (meq/100 g)	**8.34a (0.6)**	**5.7b (0.4)**	**7.2a (0.6)**	**6.7b (0.5)**	7.2 (0.6)	5.7 (0.4)	7.7 (1.1)	7.7 (0.8)	6.7 (1.1)
C:N	**14.8a (0.5)**	**19.3b (0.6)**	**15.6a (0.6)**	**18.8b (0.7)**	17.5 (1.2)	16.1 (0.9)	18.6 (1.5)	16.5 (1.0)	17.7 (1.1)
Ca:Al	2.0 (0.8)	1.0 (0.3)	**3.5a (1.1)**	**0.5b (0.1)**	1.2 (0.8)	2.0 (0.9)	3.9 (3.1)	1.3 (0.8)	2.4 (1.0)
K	**99.3a (8.9)**	**76.2b (6.0)**	**93.2a (8.3)**	**80.7b (5.7)**	**93.3ab (10.6)**	**75.8ab (4.6)**	**99.0ab (17.1)**	**105.4a (13.1)**	**65.3b (8.5)**
Mg	**63.1a (11.0)**	**27.2b (3.8)**	**58.5a (10.6)**	**29.3b (4.0)**	41.3 (11.8)	44.2 (12.2)	52.9 (18.8)	51.3 (15.9)	32.6 (10.4)
Mn	51.3 (7.3)	50.5 (6.8)	**68.6a (6.1)**	**33.1b (6.3)**	61.2 (14.6)	36.2 (6.9)	49.0 (14.3)	53.4 (9.6)	53.9 (10.0)
P	1.4 (0.1)	2.0 (0.3)	1.6 (0.1)	1.8 (0.4)	2.1 (0.3)	1.3 (0.08)	1.8 (0.4)	2.1 (0.7)	1.4 (0.2)
Fe	10.2 (2.7)	8.9 (1.7)	**6.4a (2.2)**	**12.7b (2.0)**	7.4 (1.9)	6.5 (2.1)	9.8 (4.1)	2.0 (0.2)	13.7 (5.5)
Zn	2.4 (0.2)	2.1 (0.2)	**2.0a (0.2)**	**2.4b (0.3)**	2.7 (0.3)	2.0 (0.2)	2.5 (0.6)	1.5 (0.2)	2.4 (0.4)
H/S/V Cover (%)	14.0 (2.6)	10.5 (1.4)	11.5 (1.8)	12.7 (2.3)	**7.2a (2.0)**	**8.4ab (1.7)**	**10.1ab (1.9)**	**12.5ab (2.8)**	**21.8b (4.5)**
Herb richness	**42.7a (3.8)**	**25.1b (1.8)**	35.8 (3.1)	30.8 (3.4)	28.3 (3.4)	35.7 (4.3)	30.1 (5.6)	37.1 (6.7)	34.3 (5.7)
Tree seedling richness	**16.3a (0.8)**	**11.0b (0.5)**	13.0 (0.7)	13.9 (1.0)	13.6 (1.3)	14.7 (1.0)	11.4 (1.6)	13.9 (1.3)	13.2 (1.4)
Sapling richness	**5.5a (0.7)**	**1.5b (0.2)**	2.9 (0.7)	3.8 (0.7)	3.6 (1.2)	2.4 (0.4)	3.3 (1.0)	3.8 (1.2)	3.7 (1.0)
Sapling density	**27.0a (6.0)**	**3.0b (0.8)**	12.6 (3.3)	16.3 (5.6)	1.5 (0.4)	0.7 (0.2)	0.9 (0.4)	1.5 (0.6)	2.5 (1.2)
Live tree richness	9.1 (0.6)	8.4 (0.6)	8.8 (0.5)	8.6 (0.6)	**9.9a (0.6)**	**9.9a (0.8)**	**9.5a (0.6)**	**9.2ab (0.8)**	**5.4b (0.8)**
Live tree density	59.1 (3.5)	70.0 (5.8)	62.7 (4.6)	67.2 (5.5)	**76.3a (5.5)**	**76.1a (4.6)**	**81.6a (6.9)**	**65.1a (5.7)**	**31.3b (7.0)**
Live tree basal area (m^2)	4.6 (0.3)	4.3 (0.4)	4.6 (0.4)	4.3 (0.3)	**6.1a (0.3)**	**5.7a (0.3)**	**5.0ab (0.3)**	**3.5bc (0.3)**	**2.2c (0.4)**
Dead tree richness	**2.4a (0.3)**	**3.8b (0.4)**	3.0 (0.4)	3.4 (0.4)	**3.6ab (0.5)**	**4.1a (0.7)**	**4.0ab (0.9)**	**2.7ab (0.6)**	**1.8b (0.3)**
Dead tree density	**4.5a (0.9)**	**10.2b (1.8)**	6.9 (1.3)	8.4 (1.9)	7.3 (1.7)	11.1 (0.7)	10.9 (3.4)	6.5 (1.9)	3.4 (0.7)
Dead tree basal area (m^2)	0.2 (0.05)	0.4 (0.07)	0.4 (0.07)	0.3 (0.06)	0.5 (0.1)	0.3 (0.08)	0.5 (0.2)	0.3 (0.1)	0.2 (0.04)
Litter depth (cm)	2.4 (0.1)	2.5 (0.1)	**2.6 (0.1)**	**2.3 (0.1)**	2.6 (0.2)	2.6 (0.3)	2.4 (0.2)	2.5 (0.2)	2.1 (0.1)
Soil temperature (°C)	17.9 (0.3)	18.2 (0.4)	17.9 (0.4)	18.2 (0.3)	17.3 (0.4)	18.7 (0.8)	16.6 (0.5)	18.6 (0.5)	18.8 (0.5)

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.05.037.

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